STAND STRUCTURAL DYNAMICS OF BOREAL CONIFER, MIXEDWOOD, AND BROADLEAF FIRE- AND CLEARCUT LOGGING-ORIGIN STANDS IN CENTRAL CANADA

By

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A Thesis Submitted in
Partial Fulfillment of the Requirements for the
Degree of Master of Science in Forestry

Faculty of Forestry and the Forest Environment

Lakehead University

August 2006

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Your file Votre référence
ISBN: 978-0-494-21505-0
Our file Notre référence
ISBN: 978-0-494-21505-0

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ABSTRACT

Brassard, B.W. 2006. Stand structural dynamics of boreal conifer, mixedwood, and broadleaf fire- and clearcut logging-origin stands in central Canada. 125 pp.

Key Words: biodiversity, boreal forest, chronosequence, clearcutting, coarse woody debris, downed woody debris, fire, forest management, live trees, old-growth, snags, stand structure, wildlife habitat.

Stand structure has been linked to forest regeneration, nutrient cycling, wildlife habitat, biodiversity, and climate regulation. A review and synthesis of literature indicated that boreal forest stand structure is influence by time since stand-replacing fire (TSF), stand composition, non-stand-replacing disturbances (i.e., spruce budworm and blowdown), regional differences based on climate and surficial deposit variability, and forest management. My objectives were to examine the effects of TSF, overstory composition, and stand origin (fire versus clearcutting) on living tree and coarse woody debris (CWD) (defined as snags and downed woody debris (DWD)) dynamics.

I sampled CWD in 69 stands representing typical upland conifer, mixedwood, and broadleaf stand types in the central boreal forest region of North America, ranging in age from 7 to 201 years since fire in the post-fire stands and 7 to 31 years since logging in the post-clearcut stands in northwestern Ontario, Canada. Living trees were only sampled in the 33 72 to 201 year-old fire-origin stands as most trees in younger stands did not meet my sampling criteria (diameter at breast-height (DBH) ≥10 cm).

Stand volume of trees differed with TSF with a U-shaped pattern in conifer stands, an inverse U-shaped pattern in broadleaf stands, but it did not change in mixedwoods. Tree density showed a U-shaped pattern with TSF for all stand types. For fire-origin stands, CWD volume showed a sigmoid pattern with stand age. The effect of stand type on CWD volume interacted significantly with stand age, showing that mixedwoods had the greatest CWD volume in 7 year-old stands, whereas conifer stands had highest CWD volume in 139 year-old stands. Contributions of snag and DWD volume to CWD volume also differed with stand age and stand type.

As stand age increased from 25 to 201 years, species composition of CWD shifted from dominance by early successional tree species to dominance by later successional trees species, reflecting tree species successional trajectories. Composition of DWD decay status also varied with stand age and type. In post-clearcut stands, CWD volume was smaller, mostly noncommercial tree species, and more advanced status of decay compared to post-fire stands with similar age.

Diameter at breast-height-based Shannon's index, applied to tree and snag data from 72-201 years post fire indicated that mixedwood stands were most diverse followed by conifer and then broadleaf stands while no TSF effect was found. Height-based Shannon's index showed that structural diversity peaked at a TSF of 139 years in broadleaf stands but was unaffected by TSF in conifer and mixedwood stands. While DBH-based coefficient of variation (CV) had a similar trend as height-based Shannon's index, height-based CV indicated highest diversity at a TSF of 139 years regardless of stand type.

The results of this study suggest that (a) forest management options for increasing structural diversity may include lengthening the harvest rotation and altering partial-harvesting objectives, (b) by managing stand density in post-clearcut stands the dynamics of post-fire and post-clearcut stands may converge as stand age increases, and (c) leaving a greater proportion of coniferous residual trees may allow CWD to persist for longer in the developing stand.

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ACKNOWLEDGEMENTS

I wish to give my sincere appreciation to my supervisor Dr. Han Chen for his assistance, support and guidance throughout the development of my thesis. I would also like to thank my committee members Dr. Jian Wang, Dr. Peter Duinker, and Paul Poschmann and my external reviewer Dr. Vic Lieffers. I am grateful towards Jennifer Fricker, Stephen Hart, Martina Köhler, Nick Dang, and Pat Cybulski for providing assistance in the field and laboratory and Paul Poschmann for helping with site selection in the Spruce River Forest. I would like to thank Han Chen, Jian Wang, Peter Duinker, Paul Poschmann, Dr. Gordon Kayahara, Megan Thompson, and Abby Anderson for their assistance with manuscript preparation. Funding was provided by grants from the Sustainable Forest Management Network of Centers of Excellence and the Natural Sciences and Engineering Research Council, and are greatly appreciated.

Finally, I would like to thank my parents Richard and Pauline Brassard for their love, support, and encouragement. They have been there for me through the good times and the bad, and without them, I would not be where I am today.

NOTE TO THE READER

While considerable effort has been made to integrate chapters 2, 3, and 4, these chapters have been written and submitted for publication as distinct manuscripts, and as such, there is some overlap of term definitions and repetition of methods. Chapter 2 has been published in Critical Reviews in Plant Sciences, while Chapters 3 and 4 have been submitted for publication to Canadian Journal of Forest Research and Ecological Applications respectively.

Chapter 2:
Brassard, B.W. and H.Y.H Chen. 2006. Stand structural dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25:115-137.

Chapter 3:
Brassard, B.W., H.Y.H. Chen, P.N. Duinker and J.R. Wang. Vertical structural dynamics of fire-origin boreal conifer, mixedwood, and broadleaf stands in central Canada. Canadian Journal of Forest Research (submitted April 2006).

Chapter 4:
Brassard, B.W. and H.Y.H. Chen. Coarse woody debris dynamics of boreal conifer, mixedwood, and broadleaf fire- and clearcut logging-origin stands in central Canada. Ecological Applications (submitted June 2006).

CHAPTER ONE GENERAL INTRODUCTION

Boreal forests account for 30% of the world's terrestrial phytomass (Bailey 1996). In North America, four major boreal ecozones (Atlantic Maritime, Boreal Shield, Boreal Plains, and Boreal Cordillera) form a continuous forest belt from east to west between 45° and 65° north. Of Canada's 417.6 million hectares of forest, nearly 90% of the productive forest area is boreal, which represents more than 30% of the global boreal forest (Figure 1.1).

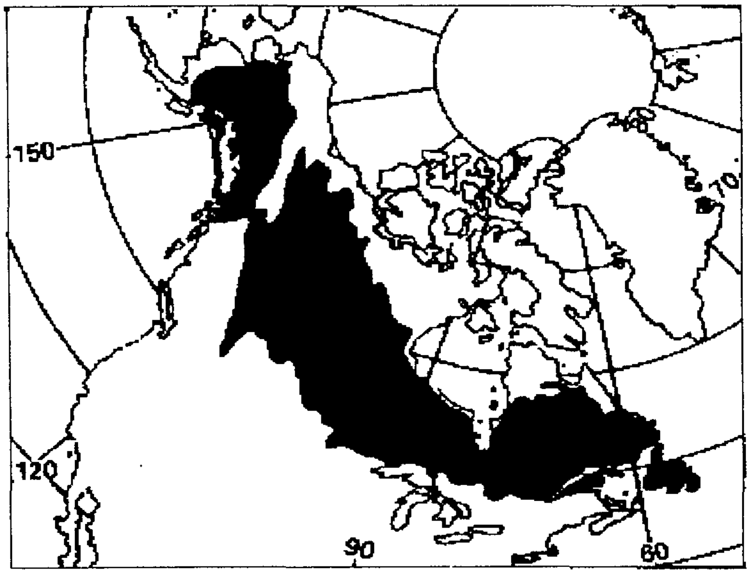

Figure 1.1. The boreal forest in North America (from Hare and Ritchie (1972)).

The boreal forest varies greatly in climate and disturbance regimes. Climates range from dry and cold climates with a mean annual temperature of only –8° C and a mean annual precipitation of 300 mm to relatively warm and moist climates with a mean annual temperature of 6° C and a mean annual precipitation of 1350 mm (Rowe 1972).

The boreal forest ecosystems today host 291 plant species distributed among 147 genera and 47 families (La Roi 1967).

In the boreal forest, fire is the most common natural stand-initiating disturbance mechanism (Johnson 1992; Weber and Stocks 1998). Fires in the boreal forest are generally large, but can range from affecting only a few to well over a hundred thousand hectares of forested land (Johnson 1992). One of the largest fires even recorded in Canada, a free-burning fire in northern British Columbia and Alberta in 1950, destroyed approximately 1.4 millions hectares of forest (Johnson 1992). Further, fire organizes plants communities, controls successional processes, and influences ecosystem functions and structures (Johnson 1992; Oliver and Larson 1996; Weber and Stocks 1998). Therefore, boreal forest succession is regulated by fire, and shows regional variation in fire characteristics and forest succession based on climate differences (which will be addressed in chapter 2) (Bergeron 1991; Johnson 1992).

Forest stand structure (defined as live tree and coarse woody debris characteristics in this thesis) is influenced by the fire event and by the time that has elapsed since the fire occurred. Research has shown that boreal forest stand structure changes as time since stand-replacing fire (TSF) increases (Paré and Bergeron 1995; Lee *et al.* 1997; Clark *et al.* 1998; Delong and Kessler 2000; Hély *et al.* 2000a; Harper *et al.* 2005). Further, studies have also indicated that these characteristics are variable between different boreal stand types (Greif and Archibold 2000; Hély *et al.* 2000b; Ferguson and Archibald 2002; Krankina *et al.* 2002; Pedlar *et al.* 2002; Varga *et al.* 2005). Examples of two common stand types occurring in my study area are: (1) jack pine (*Pinus banksiana* Lamb.)-dominated and (2) trembling aspen (*Populus tremuloides* Michx.)-dominated. These two tree species are very common in central Boreal Shield, and often form pure or mixed species stands shortly after fire (Rowe 1972). Therefore, two objectives of this thesis were to: (1) examine how forest stand structure changes as TSF increases and (2) determine if forest stand structure is affected by different stand compositions that are common in this region of the boreal forest.

In the boreal forest, clearcut logging is the most common harvesting practice, resulting in most of the trees from a stand being removed for commercial usage (Keenan and Kimmins 1993). In an attempt to offset some of the negative impacts of clearcutting on forest ecosystems, guidelines have been written with the goal(s) of creating and retaining certain structural features during clearcutting for the purpose of managing for wildlife habitat and biodiversity, retaining soil and its structure, and protecting watersheds (Ontario Ministry of Natural Resources 2001). However, it is unknown whether the structural development of post-fire and post-clearcut stands is similar (Krankina *et al.* 2002; Pedlar *et al.* 2002). Therefore, a third objective of this thesis was to determine if forest stand structural development differs in post-fire compared to post-clearcut stands. It is my hope that the finding of this thesis will help forest managers make more informed decision with regards to forest structure that are ecologically sound.

CHAPTER TWO STAND STRUCTURAL DYNAMICS OF NORTH AMERICAN BOREAL FORESTS: A REVIEW

INTRODUCTION

Stand structure, the arrangement and interrelationships of live and dead trees, is one of the key attributes of forest ecosystems. Stand structure has important implications for forest ecosystems including the maintenance of wildlife habitat (Sturtevant *et al.* 1997; Kolström 1998; Lee 1998; Ecke *et al.* 2002), the regulation of climate through carbon storing (Harmon and Hua 1991; Gower 2003), and the prevalence of forest regeneration (Siitonen *et al.* 2000). Forest stand dynamics refers to the changes in forest stand structure over time (Oliver and Larson 1996; Chen and Popadiouk 2002). These changes are driven by various stand-initiating disturbances, partial disturbances and autogenic processes (Delong and Kessler 2000). For the purpose of this chapter, the study of forest stand structure will include an examination of the physical and temporal characteristics of both live trees and coarse woody debris (CWD).

This chapter will review the stand structural dynamics of boreal forests in North America. The topics that will be covered in this review include (1) tree species compositional dynamics, (2) structural changes with time since fire (TSF), (3) the effect of canopy composition on stand structure, (4) the role of non-stand-replacing disturbances in altering forest structure, (5) variability of stand structure related to climate and geography, and (6) a comparison of stand structure in natural forests and managed forests.

TREE SPECIES COMPOSITIONAL DYNAMICS IN THE NORTH AMERICAN BOREAL FOREST

Forest stands develop by changing in composition and structure over time (Finegan 1984). Successional trends in the boreal forest depend upon differences in fire frequency (Bergeron and Dubuc 1989). An important process, for example, is cyclic succession, and occurs when the frequency of fire is short enough that species replacement does not occur, and the same species that colonized the stand after disturbance dominate until the next stand-replacing disturbance (Dix and Swan 1971; Carleton and Maycock 1978; Johnson 1992; Chen and Popadiouk 2002). This leads to the persistence of sites dominated by shade intolerant species such as jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marsh.) (Carleton and Maycock 1978; Cumming *et al.* 2000; Chen and Popadiouk 2002). In contrast, directional succession involves species replacement and leads to stands dominated by shade tolerant white and black spruce (*Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) BSP, respectively), balsam fir (*Abies balsamea* (L.) Mill.), eastern white cedar (*Thuja occidentalis* L.), and paper birch when TSF is significantly long (Bergeron and Dubuc 1989; De Grandpré *et al.* 2000; Harper *et al.* 2002; Lesieur *et al.* 2002). Species replacement is controlled by differences in a species' ability to reproduce under a closed canopy (Bergeron and Dubuc 1989), and the ability of a species to persist in the forest as succession proceeds is related to its unique ability to successfully reproduce within the changing conditions that succession creates (Suffling 1995).

Surficial deposits and landscape configuration are important contributors in determining which species colonize certain areas of forest and how succession proceeds (VanCleve *et al.* 1991; Gauthier *et al.* 2000; Chen and Popadiouk 2002; Harper *et al.* 2002). Mixedwood or broadleaf stands tend to be more abundant on mesic, modal sites while coniferous stands are more abundant on hydric and xeric sites (Bergeron and Dansereau 1993; Timoney 2003), reflecting long-term evolutionary trends. Mesic sites are usually colonized by trembling aspen (Gauthier *et al.* 2000) whereas rocky and sandy drier sites are usually dominated by jack pine (De Grandpré *et al.* 2000; Gauthier *et al.* 2000; Timoney 2003). Acidic soils create conditions where black spruce can thrive and other species are excluded due to their intolerance of acidic soils (Parisien and Sirois 2003). Over time, succession brings about a change in stand species composition, resulting in a decrease in the proportion of shade intolerant species, i.e., paper birch, trembling aspen, and jack pine in favour of an increase in the proportion of shade tolerant conifers, i.e., balsam fir, black spruce, white spruce, and eastern white cedar (Bergeron and Dubuc 1989; Bergeron and Dansereau 1993; Bergeron and Harvey 1997; Bergeron 2000; De Grandpré *et al.* 2000; Gauthier *et al.* 2000; Harper *et al.* 2002). The succession on mesic, boreal sites can be summarized as follows (Bergeron 2000; De Grandpré *et al.* 2000; Gauthier *et al.* 2000):

1. Domination of the post-fire cohort by trembling aspen and paper birch. Many boreal tree species rely on fire as a mechanism for propagation (Johnson 1992; Thompson *et al.* 1998). Paper birch and trembling aspen are early successional species that have adapted to frequent fires and open conditions by evolving regeneration mechanisms that make them well suited to quickly colonize habitats

disturbed by fire (Harper and Macdonald 2002). Paper birch and trembling aspen can reproduce by stem sprouts and suckering respectively, or by seeds (Bergeron and Dubuc 1989; Suffling 1995; Bergeron and Harvey 1997; Bergeron 2000; Vasiliauskas and Chen 2002). Paper birch is especially successful at colonizing early after fire in the absence of trembling aspen (Bergeron 2000).

2. Broadleaf (most noticeably trembling aspen) stands breakup from age-related factors and the formation of mixedwoods through an increase in conifer abundance. Trembling aspen decline has been found to occur at an age as early as 60 years after a stand-replacing disturbance (Pothier *et al.* 2004). In turn, Paré and Bergeron (1995), Cumming *et al.* (2000), and Kabzems and Garcia (2004) all revealed that trembling aspen can dominate forest stands for a considerable length of time due to its ability to recruit new individuals in gaps created during stand breakup and therefore foster the development of more than one dominating cohort. Structural heterogeneity therefore increases as stand age increases, indicating that structural development as a result of gap dynamics is not exclusive to forests composed largely of shade tolerant conifers (Cumming *et al.* 2000).
3. Increasing abundance and dominance of shade tolerant coniferous species (white spruce, balsam fir, and eastern white cedar) species and the prevalence of eastern spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks maintain a broadleaf component in the forest due to the superior competitive ability of broadleaf trees when sufficient light is available. Some species such as eastern white cedar and white spruce have not evolved unique adaptations to fire, and therefore are usually present predominantly late in succession in areas where TSF

is very long (Kneeshaw and Bergeron 1998; Asselin *et al.* 2001; Parisien and Sirois 2003).

In the North American boreal forest, jack pine and black spruce are the two most extensively distributed coniferous species (Arseneault 2001). When jack pine establishes as the pioneering cohort on xeric sites, it is usually replaced by black spruce when the fire return interval is long enough (De Grandpré *et al.* 2000; Gauthier *et al.* 2000; Harper *et al.* 2002). The pre-fire abundance of jack pine largely determines its presence in the post-fire landscape. However, long fire intervals can cause jack pine to disappear through succession to more shade tolerant species (Bergeron and Dansereau 1993). Both black spruce and jack pine use seeds as their main mechanism for reproduction (Suffling 1995; Vasiliauskas and Chen 2002) and have evolved heat-opening semiserotinous and serotinous cones respectively (Arseneault 2001; Parisien and Sirois 2003), although black spruce can also reproduce by layering (Suffling 1995).

Organic and hydric sites are predominantly colonized by black spruce, tamarack (*Larix laricina* (Du Roi) K. Koch), and eastern white cedar (Bergeron and Dubuc 1989; Gauthier *et al.* 2000; Harper *et al.* 2002). Large, extremely intense fires can create situations where large areas are burned and the establishment of jack pine or black spruce is hindered due to the large distance from a seed source or by the destruction of seeds on sites that were available for propagation before the fire (Arseneault 2001). On organic sites dominated by black spruce, species replacement is virtually absent, and the structure of the stand changes over time from a single-layered canopy to one that is multi-layered (Gauthier *et al.* 2000; Harper *et al.* 2002). However, balsam fir can be found in very old black spruce stands suggesting that changes in stand composition of black spruce dominated stands can occur (De Grandpré *et al.* 2000). On xeric sites in the southern part of the boreal forest at the limit of its northern distribution (Timoney 2003), red pine (*Pinus resinosa* Ait.) can be the dominant post-fire cohort (Bergeron and Gagnon 1987; Bergeron and Dubuc 1989). Many species such as white pine (*Pinus strobus* L.), red pine, sugar maple (*Acer saccharum* Marsh.), eastern white cedar, and yellow birch (*Betula alleghaniensis* Britt.) reach their northwestern limits in southeastern Manitoba and northwestern Ontario (Timoney 2003).

The successional trends described above apply to eastern, central and westcentral North American boreal forests. In Alaska, topography is even more important in controlling stand composition and structure while soil parent materials and disturbance regimes all contribute to tree species compositional dynamics (Viereck *et al.* 1983; VanCleve *et al.* 1991; VanCleve *et al.* 1996). In the sub-boreal forest of British Columbia, stands are usually colonized by lodgepole pine (*Pinus contorta* Dougl. ex Loud.) (an early successional species with serotinous cones) following fire, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and hybrids of white spruce and Engelmann spruce (late successional species) can form dominant stands as well (Clark *et al.* 2003). Even when the establishment densities of lodgepole pine are low, this species usually dominates due to its ability to grow more rapidly than its associated more shade tolerant species (Chen *et al.* 1996; Chen 1997; Clark *et al.* 2003). Like jack pine, however, lodgepole pine can disappear from the landscape due to its inability to establish itself beyond stand-replacement (Chen 1997; Antos and Parish 2002) especially when fire return intervals are long, very intense fires destroy seed sources, and/or recruitment from distant stands is difficult (Clark *et al.* 2003). Over time, the ability of subalpine fir and white spruce and Engelmann hybrids to grow in the understory and subcanopy will result in their increased abundance at the expense of lodgepole pine (Clark *et al.* 2003). Subalpine fir dominates older forests due to its efficient seed bank and shade tolerance (Antos and Parish 2002). Although old stands are largely dominated by subalpine fir, white spruce and Engelmann hybrids can establish in the understory and be an important component of the overstory in even the oldest stands (Varga and Klinka 2001; Clark *et al.* 2003).

STRUCTURAL CHANGES IN THE BOREAL FOREST WITH TIME SINCE FIRE

Stand structure includes characteristics of both live trees and coarse woody debris (CWD) (defined as snags and downed woody debris (DWD)) (Table 2.1). In this section, I evaluate stand structural dynamics through the changes of both live trees and CWD in stand basal area (BA), volume, density, abundance, spatial and size distribution, decay state (CWD only), and species composition along chronosequences.

Living Tree Dynamics

Young stands contain trees with small tree heights and small diameters although large, live, residual trees do often survive stand-replacing fires and continue to grow in the post-disturbance stand (Greif and Archibold 2000). The density of trees in a stand decreases while tree size increases with stand age (Lee *et al.* 1997; Delong and Kessler 2000; Popadiouk *et al.* 2003). Therefore, older forest stands contain larger trees than younger stands, but have less overall trees per unit area (Delong and Kessler 2000). This is a result of the self-thinning process, as competition between stems and unequal success at utilizing resources allows some stems to survive and continue to grow while others perish (Oliver and Larson 1996; Chen and Popadiouk 2002). Consequently, the stand

Table 2.1. Dynamics of live trees and coarse woody debris (CWD) in boreal forests.

Study	Stand age (years)	Stand type*	Stand origin†	Live trees			CWD						Location
								Snags			DWD‡		
				Volume (m^3/ha)	Density (stems/ha)	Basal area (m^2/ha)	Total volume (m^3/ha)	Volume (m^3/ha)	Density (stems/ha)	Basal area (m^2/ha)	Volume (m^3/ha)	Density (stems/ha)	
North American boreal forests:													
Clark *et al.* (1998)	0-50	C	F							32	>100		sub-boreal, British Columbia
Reich *et al.* (2001)	25-40	C	F			23							southern boreal, Minnesota
DeLong and Kessler (2000)	40-70	C	F		2597				268		262		sub-boreal, British Columbia
Clark *et al.* (1998)	51-100	C	F							2			sub-boreal, British Columbia
Clark *et al.* (1998)	51-200	C	F								60		sub-boreal, British Columbia
DeLong and Kessler (2000)	71-140	C	F		1910				460		174		sub-boreal, British Columbia
Ruel *et al.* (2004)	77-90	C	F	263-376	1967-2850	37-47							central Quebec
Reich *et al.* (2001)	70-100	C	F			27							southern boreal, Minnesota
Pedlar *et al.* (2002)	88	C	F				18						northwestern Ontario
DeLong and Kessler (2000)	>140	C	F		984				170		193		sub-boreal, British Columbia
Stewart *et al.* (2003)	164-214	C	F	540-563	497-520	56-58	110-148	40-57	47-149	5-8	71-91		Nova Scotia
Clark *et al.* (1998)	201-250	C	F							12			sub-boreal, British Columbia
Hély *et al.* (2000b)	236	C	F			35					34		northwestern Quebec
Clark *et al.* (1998)	≥400	C	F								143		sub-boreal, British Columbia
Ferguson and Archibald (2002)	0-60	C	H		14-17				1-2				northwestern Ontario
Brumelis and Carleton (1988)	1-56	C	H		3050								northeastern Ontario
Reich *et al.* (2001)	25-40	C	H			20							southern boreal, Minnesota
Sturtevant *et al.* (1997)	36	C	H								32		Newfoundland
Ruel *et al.* (2004)	49-55	C	H	75-173	1250-1608	14-27							central Quebec
Ferguson and Archibald (2002)	61-80	C	H		26-31				2-4				northwestern Ontario

Table 2.1. (Continued).

Sturtevant *et al.* (1997)	64	C	H								15		Newfoundland
Reich *et al.* (2001)	70-100	C	H			31							southern boreal, Minnesota
Sturtevant *et al.* (1997)	80	C	H								78		Newfoundland
Ferguson and Archibald (2002)	81-100	C	H		25-30				3-5				northwestern Ontario
Ferguson and Archibald (2002)	>100	C	H		22-25				3-6				northwestern Ontario
Pedlar *et al.* (2002)	1	M	F				343						northwestern Ontario
Pedlar *et al.* (2002)	75	M	F				161						northwestern Ontario
Hély *et al.* (2000b)	175-205	M	F			26-37					45-52		northwestern Quebec
Ferguson and Archibald (2002)	0-60	M	H		17-18				4				northwestern Ontario
Ferguson and Archibald (2002)	61-80	M	H		23-28				4				northwestern Ontario
Ferguson and Archibald (2002)	81-100	M	H		21-25				4-6				northwestern Ontario
Ferguson and Archibald (2002)	>100	M	H		18-21				5-6				northwestern Ontario
Lee *et al.* (1997)	20-30	B	F		278				33		109	36	northeastern Alberta
Lee (1998)	20-39	B	F						18				Alberta
Reich *et al.* (2001)	25-40	B	F			22							southern boreal, Minnesota
Lee *et al.* (1997)	50-65	B	F		1247				73		109	32	northeastern Alberta
Pedlar *et al.* (2002)	67	B	F				105						northwestern Ontario
Reich *et al.* (2001)	70-100	B	F			26							southern boreal, Minnesota
Lee (1998)	≥100	B	F						62-100				Alberta
Hély *et al.* (2000b)	117	B	F			46					40		northwestern Quebec
Lee *et al.* (1997)	≥120	B	F		535				66		124	31	northeastern Alberta
Stewart *et al.* (2003)	178-197	B	F	269-300	366-461	33-38	62-84	17-25	11-100	3-4	45-58		Nova Scotia
Ferguson and Archibald (2002)	0-60	B	H		14				3				northwestern Ontario
Reich *et al.* (2001)	25-40	B	H			19							southern boreal, Minnesota
Ferguson and Archibald (2002)	61-80	B	H		27				4				northwestern Ontario
Reich *et al.* (2001)	70-100	B	H			31							southern boreal, Minnesota
Ferguson and Archibald (2002)	81-100	B	H		30				5				northwestern Ontario

Table 2.1. (Continued).

Ferguson and Archibald (2002)	>100	B	H		25				5				northwestern Ontario
European and Asian boreal forests:													
Linder *et al.* (1997)	117-270	C	F	108-511	1106-2889			12-70	167-334		31-166	88-366	boreal Sweden
Siitonen *et al.* (2000)	129-198	C	F	396	725	35	111						southern Finland
Rouvinen *et al.* (2002)	187-210	C	F	151-333			59-92	24-47			20-52		boreal Fennoscandia
Kuuluvainen *et al.* (1998)	>200	C	F	216	2064		145	28	263		117		northeastern Europe
Karjalainen and Kuuluvainen (2002)	>250	C	F				70	27	75		43		Russian Viena Karelia
Narukawa *et al.* (2003)	>300	C	F									176	Taisetsu, Japan
Jonsson (2000)	old-growth	C	F					1-13			17-65		northern Sweden
Sippola *et al.* (1998)	old-growth	C	F				19-60	7-11			11-47		Finnish Lapland
Rouvinen *et al.* (2002)	111-179	C	H	156-169			7-22	2			5-20		boreal Fennoscandia
Siitonen *et al.* (2000)	124-145	C	H	331	801	31	22						southern Finland
Siitonen *et al.* (2000)	95-118	C	H	299	605	28	14						southern Finland
Sippola *et al.* (1998)	15	C	H				8	1			7		Finnish Lapland
Takahashi *et al.* (2001)	≥120	M	F		1071	26							Kamchatka peninsula, Russia
Linder *et al.* (1997)	88-108	B	F	87-218	1154-1981			12-31	318-621		16-80	135-223	boreal Sweden

*Stand type: C = conifer, M = mixedwood, B = broadleaf

†Stand origin: F = fire, H = managed

‡DWD = downed woody debris

changes from having a largely uniform, single-layered canopy with stems that are relatively homogenous in diameter and height to having a bimodal or multi-modal canopy structure with a broad, multi-sized diameter and height distribution with dominance of shade tolerant tree species (Paré and Bergeron 1995; Linder *et al.* 1997; Kuuluvainen *et al.* 1998; Varga and Klinka 2001; Clark *et al.* 1998).

In forest stands, the spatial pattern of live trees is a reflection of initial establishment patterns, sunlight and climatic variables, interspecific and intraspecific competition, microenvironment, and chance (Moeur 1993). In boreal and other temperate forests, the spatial arrangement of live trees has been reported as shifting from a clumped distribution in young stands to a relatively regular distribution in older stands (Kenkel 1988; Moeur 1993; Szwagrzyk and Czerwczak 1993; Kenkel *et al.* 1997; Chokkalingam and White 2001; Gratzer and Rai 2004), a consequence of density-dependent intraspecific competition between neighboring stems during self-thinning. However, other studies suggest that the establishment of trees on microsites and canopy gaps and the regeneration strategies of some tree species (i.e., vegetative reproduction such as stem sprouting, limited seed dispersal ability, and preferential establishment on DWD) in intermediate-aged and older stands can cause the structural patterns of trees to become relatively clumped (Payandeh 1974; Taylor and Halpern 1991; Peterson and Squiers 1995; Camarero *et al.* 2000; Manabe *et al.* 2000; Takahashi *et al.* 2001; Hou *et al.* 2004). A random spatial arrangement of trees in intermediate-aged and old stands may be attributed to weak competition or clumping processes (Szwagrzyk and Czerwczak 1993; Wallenius *et al.* 2002). Further, disturbances beyond stand-replacement (i.e., insect outbreaks, blowdown, and pathogen infections) (Szwagrzyk and Czerwczak 1993) and environmental heterogeneity (Antonovics and Levin 1980) can mask expected spatial patterns. It is unclear how the spatial arrangement of trees affects or is affected by ecological processes such as productivity, disturbance dynamics, and interrelationships among tree species.

Popadiouk *et al.* (2003) reported that stand BA increases with stand aging in eastern boreal mixedwoods. Similarly, Paré and Bergeron (1995) reported that, along a chronosequence, biomass increased steadily before decreasing and stabilizing. This biomass accumulation pattern appears to be a reflection of both the contribution of trembling aspen to stand composition and spruce budworm outbreaks (Paré and Bergeron 1995). In an inter-regional study of boreal, temperate, and tropical biomes using long-term chronosequences, Wardle *et al.* (2004) found that stand BA and ecosystem biomass increased, reached a maximum, and then declined in all ecosystem types. For each of the chronosequences, the decline phase was associated with an increase in the substrate nitrogen-to-phosphorus ratio, indicating increasing phosphorus limitation over time. Wardle *et al.* (2004) further concluded that the maximal biomass phase during succession cannot be maintained in the long-term absence of major disturbance in forested ecosystems spanning the tropical, temperate, and boreal zones.

The species composition and size distributions of CWD reveals the past history of a stand (Linder *et al.* 1997), which is the premise of so-called stand reconstruction approach that has been extensively used in the study of successional dynamics (Johnson and Fryer 1989; Bergeron 2000). A lesser amount of live tree volume than CWD volume of a certain tree species indicates that this species was more abundant in an earlier successional stage and is currently experiencing a decline in its contribution to stand composition (De Grandpré *et al.* 2000; Pham *et al.* 2004).

It has been reported that there is a positive relationship between the volume and BA of CWD and that of living trees (Sippola *et al.* 1998; Ferguson and Archibald 2002; Stewart *et al.* 2003). This relationship does not appear to be influenced by forest age or type (Ferguson and

Archibald 2002). Ratios of CWD to living trees vary across a wide range. For example, Nilsson *et al.* (2002) calculated a ratio of dead to live standing stems of 1:9 in the boreal forest. Siitonen *et al.* (2000) found that CWD comprises about one quarter of the total stand volume, while Kuuluvainen *et al.* (1998) found this value to be approximately 40%. Linder *et al.* (1997), Sippola *et al.* (1998), and Karjalainen and Kuuluvainen (2002) reported that CWD comprises between 19% and 30% of the total volume of timber in old-growth forests. However, Rouvinen *et al.* (2002) did not find a relationship between CWD and live tree volume. It is unclear how competition and longevity-induced mortality and species-specific rates of CWD decomposition contribute to the discrepancies in the ratio of CWD to live tree volume.

CWD Dynamics

The CWD in a stand can influence nutrient cycling, productivity, and species composition (Spies *et al.* 1988; Greif and Archibold 2000; Karjalainen and Kuuluvainen 2002). The CWD dynamics is largely a reflection of the TSF (Arseneault 2001), as fire is the main disturbance factor in the boreal forest (Johnson 1992; Linder *et al.* 1997; Amiro *et al.* 2001; Amiro *et al.* 2002; Karjalainen and Kuuluvainen 2002) for both producing and eliminating dead organic material in forests under natural conditions (Sippola *et al.* 1998). Fires in the boreal forest can be either lethal, killing most of the trees in a stand and initiating a new stand, or non-lethal, killing some of the trees in the stand (Johnson 1992).

Living trees, upon death, add to the CWD component in forest ecosystems (Hély *et al.* 2000a). The life history of a tree typically consists of (1) living tree, (2) snag, (3) fall of snag to the forest floor, and (4) decomposition of the downed log (Storaunet and Rolstad 2002). The processes that influence CWD are inputs through mortality and breakage (which control accumulation) and decomposition and combustion (which affect losses from the system). Inputs of CWD come from both the pre-disturbance and current stand, and the inputs from each to the total CWD pool varies with the age of the stand (Siitonen *et al.* 2000).

In the boreal forest (Sturtevant *et al.* 1997; Clark *et al.* 1998; Hély *et al.* 2000a; Ferguson and Archibald 2002) and subalpine forest (Spies *et al.* 1988), the pattern of CWD accumulation over time has been shown to follow a sigmoid distribution (Figure 2.1), where large, pre-fire in origin inputs of CWD decreases logarithmically while post-fire inputs increase exponentially (before decreasing) (Figure 2.1) (Spies *et al.* 1988; Sturtevant *et al.* 1997; Delong and Kessler 2000). This translates to high amount of CWD in young, early successional forests and old, late successional forests and low levels in mature, intermediate-aged forests, with levels in very old forests being lower than old forests (Spies *et al.* 1988; Sturtevant *et al.* 1997).

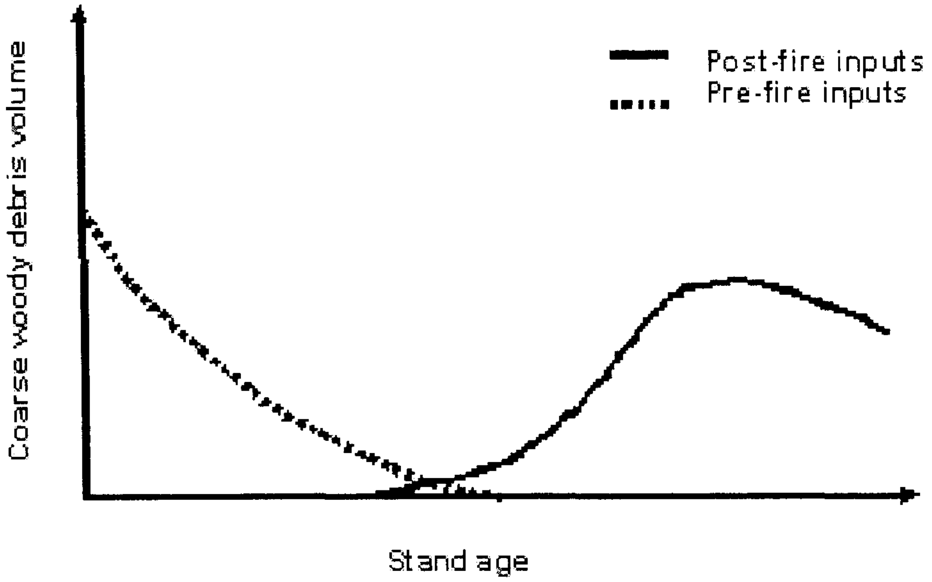

Figure 2.1. Dynamics of pre-disturbance and post-disturbance CWD patterns in a forest stand with time since fire (from Sturtevant *et al.* (1997)).

Coarse woody debris (pre-disturbance debris) and live trees (residual standing trees) can survive fire and contribute significantly to post-disturbance structure (Lee *et al.* 1997; Fraver *et al.* 2002). Residual snags will slowly deteriorate as the forest ages and fall to the ground (Greif and Archibold 2000). In young stands, the amount of CWD contributed by the pre-disturbance stand is high (Spies *et al.* 1988; Sturtevant *et al.* 1997; Clark *et al.* 1998; Delong and Kessler 2000). This includes both pre-disturbance debris that is not consumed by the stand-replacing fire and disturbance generated debris (Sturtevant *et al.* 1997). However, as the stand ages, this dead material decomposes and is incorporated into the soil (Sturtevant *et al.* 1997; Pedlar *et al.* 2002).

Coarse woody debris of post-disturbance origin is very low in young stands (Spies *et al.* 1988; Sturtevant *et al.* 1997), as trees that establish are growing to fill available growing space. During this stage of development, called stand initiation (Oliver and Larson 1996; Chen and Popadiouk 2002) the low competition-induced mortality between stems results in little inputs of CWD. In early, intermediate-aged forests, all available growing space is occupied and the trees undergo intense competition for space and resources (stem exclusion stage (Oliver and Larson 1996; Chen and Popadiouk 2002)) in self-thinning, which brings about tree mortality and causes the levels of CWD with post-disturbance origin to begin to increase (Sturtevant *et al.* 1997; Fraver *et al.* 2002). In dense, regenerating forests, there is intense competition for space, soil nutrients, moisture and light by young trees (Greif and Archibold 2000). Through self-thinning, many small snags are created as weaker trees are killed off, creating improved growing conditions for remaining trees that survive (Greif and Archibold 2000). At this point, a large proportion of CWD from the pre-disturbance stand may have disappeared while the production of CWD from the current stand has yet to occur significantly (Spies *et al.* 1988), which can explain the low levels of CWD during this stage of production.

As succession and stand development continues, stem competition ends and the colonizing cohort of trees that dominate the canopy begin to reach their maximum life expectancy and die (Chen and Popadiouk 2002). In this stage, called canopy transition (Chen and Popadiouk 2002), CWD accumulation continues to increase and the input of CWD that is post-disturbance in origin rises (Sturtevant *et al.* 1997) in these late, intermediate-aged stands. At the end of this stage when the final trees from the colonizing cohort die (Chen and Popadiouk 2002), the amount of CWD reaches its maximum while the stand undergoes a transition from an even-aged to an uneven-aged structure (Sturtevant *et al.* 1997; Hély *et al.* 2000a). After this, the stand enters the stage of old-growth when gap dynamics are predominant (Chen and Popadiouk 2002), and the amount of CWD begins to decline slightly (Sturtevant *et al.* 1997). However, new inputs of CWD continue to occur due to non-stand-replacing disturbances such as insect damage, disease, injury that is caused by neighboring trees falling, ice, snow, and wind (Greif and Archibold 2000). These will be discussed in greater detail later.

As the majority of the literature breaks down the chronosequence into young/mature, intermediate/overmature, and old/old-growth forest classes when discussing forest stand structure, this paper will do the same. For the remainder of this section, an overview of how CWD characteristics change along the chronosequence will be undertaken.

Snags

During the different stages of succession, snags have different size distributions and decay characteristics. Snags produced by a stand-replacing fire are often large (Lee *et al.* 1997). In contrast, snags produced later in succession through competition-induced stem death (self-thinning) during the stem exclusion development stage (Chen and Popadiouk 2002) tend to be smaller (Lee *et al.* 1997). Still later in succession, during the canopy transition stage of development (Chen and Popadiouk 2002), snags are a result of age-related tree mortality (Chen and Popadiouk 2002) and are once again larger in size. In old stands (gap dynamics development stage (Chen and Popadiouk 2002)), snags are produced by non-stand-replacing disturbances such as insect attacks, disease, or damage by ice, snow, and wind that may affect overmature individuals (Clark *et al.* 1998; Greif and Archibold 2000; Hély *et al.* 2000a). Unlike competition and suppression, which create small diameter snags in young stands, these factors are not size specific, and a greater range of snag diameters occurs in older stands (Greif and Archibold 2000).

The BA (i.e., the sum of cross-sectional area at breast-height per hectare, m^2/ha) and density (stems/ha) of snags both follows a sigmoid distribution over stand age, where BA and density are highest in young post-fire stands, lowest in young intermediate-aged stands, higher in older intermediate-aged stands, and reach another maximum in old stands before decreasing slightly in very old stands (Lee *et al.* 1997; Clark *et al.* 1998) (Figure 2.2). The high values for snag BA and density reported for young stands is attributed to large inputs from the pre-fire, whereas the low values that occur in young intermediate-aged stands are a consequence of snags falling to the forest floor where they become DWD and before significant post-fire inputs can occur (Clark *et al.* 1998) beyond a young intermediate age, values of snag BA and density once again increase, induced by stem competition mortality (Oliver and Larson 1996; Chen and Popadiouk 2002), trees reaching their maximum life expectancy and dying, as is the case for trembling aspen (Pothier *et al.* 2004) and lodgepole pine (Clark *et al.* 1998), or from non-stand-replacing disturbances (Clark *et al.* 1998; Greif and Archibold 2000; Hély *et al.* 2000a).

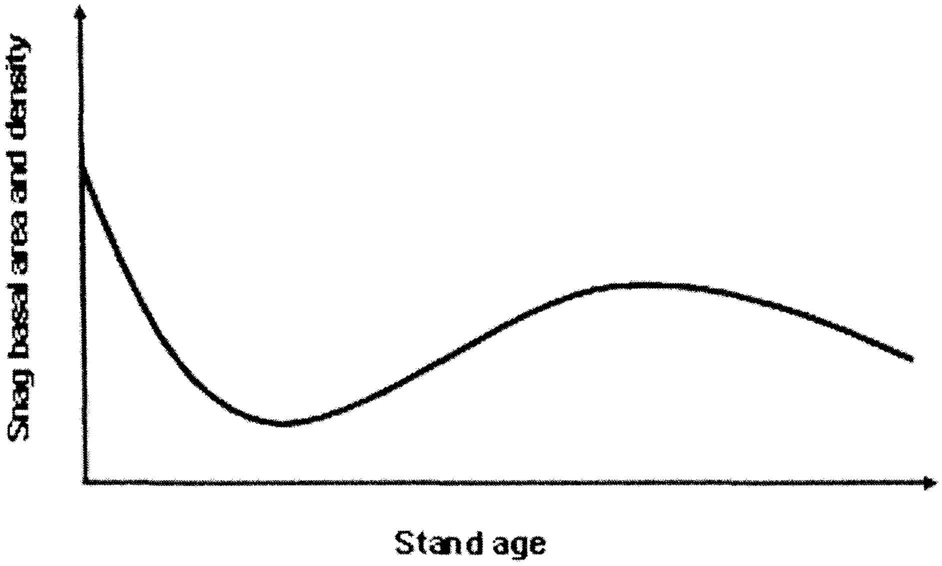

Figure 2.2. Dynamics of stand basal area and density of snags with time since fire.

DWD

Downed woody debris is important for many reasons including re-cycling nutrients into the ecosystems following disturbances (Harmon and Hua 1991; Karjalainen and Kuuluvainen 2002), storing water (Fraver *et al.* 2002; Karjalainen and Kuuluvainen 2002), fostering tree regeneration (Hofgaard 1993; Takahashi 1994; Parent *et al.* 2003; Lampainen *et al.* 2004), and sheltering and feeding small mammals (Tallmon and Mills 1994; Pearce and Venier 2005). Downed woody debris creates conditions where light and moisture requirements are favorable for tree regeneration while plant competition is limited (Kuuluvainen and Juntunen 1998; Parent *et al.* 2003). The amount of decayed DWD on the forest floor has been positively correlated to spruce, fir, and pine seedling occurrence (Webb 1988; Hofgaard 1993; Takahashi 1994; Kuuluvainen and Juntunen 1998; Narukawa *et al.* 2003; Parent *et al.* 2003; Lampainen *et al.*

2004). However, Kuuluvainen *et al.* (1998) reported that sapling density was not related to the amount of DWD on the forest floor, suggesting the DWD are favorable substrates for tree germination, but not necessarily the best medium for tree growth and survival.

Substrate quality (soil moisture and temperature), in addition to light availability (Chen *et al.* 1996; Chen 1997; Kolström 1998; Messier *et al.* 1999), is important for tree seedlings to establish. More decayed DWD show a greater occurrence of seedlings and samplings than less decayed DWD, as seedling have difficulty establishing on young logs that are relatively intact (Narukawa *et al.* 2003). Freshly fallen spruce logs take approximately 50 years to decompose to a point where spruce seedling establishment is possible (Hofgaard 1993). This is likely because freshly fallen logs have bark and wood that is too hard and cannot be utilized by tree seedlings, whereas more decomposed wood is often softer, which allows for penetration of the log by seedling roots (Narukawa *et al.* 2003). Further, some tree species (e.g., paper birch) have a persistent papery bark that makes colonization difficult (Webb 1988). Log size is also related to regeneration, as seedlings were found to be more abundant on larger logs than smaller logs because of their difference in available surface areas to seeds (Takahashi 1994).

The cross-sectional area of DWD has been found to be U-shaped in distribution, where it is highest in young stands, lowest in intermediate-aged stands, and increased to another maximum in old stands (Clark *et al.* 1998). In contrast to snag BA, the BA area of DWD continues to increase in very old stands (Clark *et al.* 1998).

The density of DWD (stems/ha) changes over time, but its pattern depends on the size of the logs. Lee *et al.* (1997) found that the density of large diameter DWD displays a U-shaped pattern along the chronosequence, the density of medium diameter DWD decreases with stand age, and the density of small diameter DWD shows an inverse U-shaped pattern as TSF increases.

The volume of DWD has been found to follow a U-shaped distribution along the chronosequence, where levels are high in young and old stands and low in intermediate-aged stands (Lee *et al.* 1997; Sturtevant *et al.* 1997; Clark *et al.* 1998) (Figure 2.3). Further, in old forests, the volume of large DWD is significantly higher than the volume of small DWD (Edman and Jonsson 2001), and by the old-growth stage, the volume of DWD has been shown to be higher than the volume of snags (Siitonen *et al.* 2000).

Decomposition of CWD

The decomposition of CWD has been shown to occur in two successive stages (1) time from the death of the tree until it falls, and (2) time after fall until decomposition is complete (Storaunet and Rolstad 2002). In young stands, there is generally a high proportion of CWD volume, BA, and density (Spies *et al.* 1988; Delong and Kessler 2000; Yatskov *et al.* 2003) that occurs in advanced states of decay compared to early states of decay. In contrast, old stands have more CWD volume, BA, and density in early decay classes compared to late decay classes (Spies *et al.* 1988; Clark *et al.* 1998; Delong and Kessler 2000; Yatskov *et al.* 2003). Coarse woody debris in old forests is also more often evenly distributed among the decay classes (Delong and Kessler 2000; Jonsson 2000; Karjalainen and Kuuluvainen 2002), although Edman and Jonsson (2001) found that the majority of DWD in old-growth coniferous forests were in intermediate to late decay classes.

The size of CWD has an effect on the volume and decay state of CWD in a stand. The volume of CWD that is large and showing little decay is higher in older stands compared to younger stands (Delong and Kessler 2000). Consequently, the volume of CWD that is small and

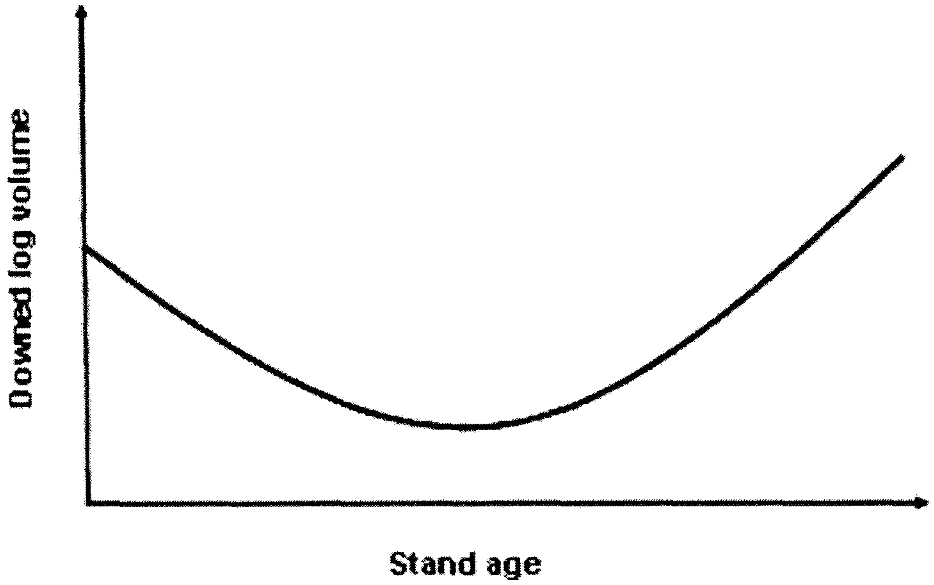

Figure 2.3. Dynamics of stand volume of downed logs with time since fire.

highly decayed is higher in younger stands compared to older stands, likely because as TSF increases, the size of dying trees also increases (Delong and Kessler 2000). Large diameter DWD appears to decay slower than small diameter DWD due to their larger size (Storaunet and Rolstad 2002), although it has been noted that the opposite occurs, attributed to large diameter DWD being in greater contact with the ground than small diameter DWD (Næsset 1999).

Decomposition of DWD is affected by substrate quality, temperature, moisture, and type and amount of decomposing organisms (Storaunet and Rolstad 2002). For example, temperature affects decay-susceptible species but not decay-resistant species (Yatskov *et al.* 2003). For decay-susceptible species, decomposition increases exponentially with increases in temperature (Yatskov *et al.* 2003). Further, decomposition rates for DWD have been reported as being higher on moist soils than drier soils (Næsset 1999). Snags in general have slower rates of decomposition than DWD (Karjalainen and Kuuluvainen 2002; Storaunet and Rolstad 2002; Yatskov *et al.* 2003), attributed to insufficient moisture in snag tissues (Yatskov *et al.* 2003). In summary, Yatskov *et al.* (2003) highlights the variations in CWD decay patterns for various species, and identifies four patterns of CWD loss (based on a 5 decay class system where decay extent increases from decay class 1 to decay class 5):

1. For *Betula* spp., a linear, gradual decrease in wood density occurs from decay class 1 to 5 which is likely caused by the prolonged retention of bark that hinders decomposition of sapwood and to the absence in the heartwood of decay-suppressing substances (Webb 1988; Yatskov *et al.* 2003). For example, European white birch (*Betula pendula* Roth) does not lose its bark during decomposition, which prevents sloughing of heartwood and sapwood cells (Yatskov *et al.* 2003).
2. For some *Pinus* spp. and *Larix* spp., very little change in wood density occurs until a decay class of 4 is reached due to the presence of dense, decay resistant heartwood, and because bark and less resistant sapwood fall off during decomposition (Yatskov *et al.* 2003).
3. For *Picea* spp. and other *Pinus* spp., decomposition and a decrease in density proceeds through a slow, rapid, and moderately slow phase (Harmon *et al.* 2000) as the breakdown of woody debris goes through the 5 decay classes. The little change in wood density that is observed in the "slow phase" (occurring between decay classes 1 and 2) is attributed to the slow colonization by decomposing organisms or to drying due to shrinkage. The large loss of density in the "rapid phase" (occurring between decay classes 3 and 4) and slight density decline (occurring between classes 4 to 5) is the result of the slow decay of remnant decay-resistant tissues (Yatskov *et al.* 2003).

4. For *Quercus* spp. and *Acer* spp., decomposition is usually complex, as decay of snags and DWD is from the log circumference towards the center. CWD of these species generally have fast initial losses of wood density due to their susceptibility to heartwood rot (Yatskov *et al.* 2003). *Acer* spp. and *Quercus* spp. lose their bark swiftly during the process of decomposition (Yatskov *et al.* 2003).

Decay characteristics are likely to have important implications for seedling establishment. In spruce forests, once the sapwood rots and thick bark falls off, available nutrients may provide ideal conditions for the establishment and growth of seedlings (Sollins 1982). However, for trees that have thinner bark (such as balsam fir), bark that remains intact long after the sapwood and heartwood rots may result in poorer conditions for seedling establishment (Sollins 1982).

THE EFFECT OF CANOPY COMPOSITION ON STAND STRUCTURE

Stand structure may differ significantly among stand types as canopy composition influences ecosystem productivity (Chen *et al.* 2003), carbon and nutrient dynamics (Simard *et al.* 1997; Prescott *et al.* 2000; Laiho and Prescott 2004), and susceptibility to natural disturbances (Su *et al.* 1996; Cumming *et al.* 2000). Some studies of boreal forests have characterized stand structure over time of live and dead material in exclusively coniferous forests (Linder *et al.* 1997; Clark *et al.* 1998) or exclusively broadleaf forests (Lee *et al.* 1997; Lee 1998), but no study has examined changes in mixedwood structure along a chronosequence in the boreal forest. The studies that have explored differences among stand types have occurred under different environmental conditions (i.e., soils, topography, geography, climate, etc.) and/or have only examined forests that are in a specific successional stage (i.e., old-growth) (Harmon and Hua 1991; Greif and Archibold 2000; Pedlar *et al.* 2002; Stewart *et al.* 2003), although Ferguson and

Archibald (2002) reported changes in snag and live tree density along the chronosequence in various boreal stand types.

While the abundance of coniferous species increases with TSF at the expense of broadleaf species (Bergeron and Dubuc 1989; Bergeron and Dansereau 1993; Bergeron and Harvey 1997; Bergeron 2000; De Grandpré *et al.* 2000; Gauthier *et al.* 2000; Harper *et al.* 2002), old mixedwood stands are still maintained in some areas due to outbreaks of spruce budworm and other disturbances that kill late successional shade tolerant coniferous species and favour the recruitment of early successional, shade intolerant broadleaf species within the canopy openings (Bergeron and Dansereau 1993). Stands dominated by broadleaf trees may be maintained if fires are relatively frequent. However, with the increase in the fire cycle (defined as "the number of years required to burn over an area equal to the whole area of the forest" (Van Wagner 1978)) that is expected to occur due to climate change for some areas of the boreal forest (Bergeron and Flannigan 1995; Flannigan *et al.* 1998; Bergeron *et al.* 2004), there is concern that pure broadleaf stands will dramatically decrease in abundance (Bergeron and Dansereau 1993). Therefore, there is a need to explore stand structural characteristics (e.g., CWD and live tree abundance, volume, density, height, diameter, and arrangement) along successional gradients for the various stand types that occur within the boreal forest. This section will synthesize information on differences in live tree and CWD structural characteristics between different boreal stand types and explore how these aspects change along a chronosequence.

Living Tree Dynamics

The BA of living trees differ among stand types (Chen and Popadiouk 2002; Popadiouk *et al.* 2003). Hély *et al.* (2000b) reported that the BA of live trees is higher in broadleaf forests than coniferous forests with mixedwood forests being intermediate. Linder (1998) also reported that live tree BA is higher in mixedwood stands compared to coniferous stands. The higher BA of live trees in broadleaf and mixedwood forests compared to coniferous forests may be explained by the superior height of trembling aspen and by the decrease in above-ground biomass that is observed to occur as a stand succeeds from broadleaf dominance into coniferous dominance (Paré and Bergeron 1995; Bergeron and Harvey 1997). However, Stewart *et al.* (2003) conversely reported that the BA of live trees was higher in coniferous stands compared to broadleaf stands.

The density and volume of live trees appears to be variable with stand type. In young stands, the density of live trees was found to be highest in coniferous stands followed by mixedwood stands and broadleaf stands (Ferguson and Archibald 2002). In old forests, coniferous stands have been reported as having a higher density of live trees than broadleaf and mixedwood stands (Linder 1998; Stewart *et al.* 2003). In turn, live tree volume has been found to be lower in old broadleaf stands than old mixedwoods and coniferous stands (Linder 1998; Stewart *et al.* 2003).

The conflicting results may reflect the confounding effects of stand type and site quality. The broad classification of coniferous *versus* broadleaf stand types may further cloud the effect of tree species dominance on stand BA and stem density. For example, these stand attributes differ significantly between broadleaf trembling aspen and paper birch-dominated stand types (Chen and Popadiouk 2002) and among coniferous stand types (Varga *et al.* 2005). Future research may require consideration of site quality and individual species dominance.

Variability of tree size within a stand is an important structural attribute as it affects forest productivity, plant diversity, and wildlife habitat (Berger and Puettmann 2000; Staudhammer and Lemay 2001; Sullivan *et al.* 2001; Pommerening 2002). Tree size diversity has been measured by using Shannon's index (Shannon and Weaver 1949), variance, standard deviation, and coefficient of variation of tree heights and diameters (Staudhammer and Lemay 2001; Varga *et al.* 2005). After studying three types of coniferous mixtures in western Canada, Varga *et al.* (2005) reported that tree-size diversity did not only differ with tree species dominance and stand age, but also increased in mixtures of shade intolerant and shade tolerant species.

Mortality Mechanisms, Canopy Gaps, and Regeneration Patterns

The kind of mortality that a tree undergoes appears to be linked to stand type. Trees in coniferous forests are more likely to be snapped than uprooted, attributed to the heavy snow loading that conifers experience (Clark *et al.* 1998; Storaunet and Rolstad 2002). However, Siitonen *et al.* (2000) and Antos and Parish (2002) found that pines usually form intact snags when they die. In contrast, spruce has been found to uproot or snap close to the ground and form logs upon death (Siitonen *et al.* 2000). In broadleaf forests, trees have a tendency to die and remain as snags rather than being uprooted or breaking (Lee 1998), although Siitonen *et al.* (2000) has reported that broadleaf trees have a tendency to snap and break. A study of trembling aspen gap dynamics 60 to 120 years since fire in eastern boreal forests reported that snags were most frequent in young stands, whereas snapped snags were most frequent in old stands (Hill *et al.* 2005). Infection by fungal pathogens was the most frequent cause of mortality (56%), followed by blowdown (16%), and all other causes including mammals, insects, and those unidentified (28%) (Hill *et al.* 2005).

Gaps appear to be important in seedling establishment, as recruitment has been found to be very poor (restricted to shade tolerant species) under a closed canopy (Coates 2002). The species of gap makers and gap fillers differ between coniferous and broadleaf stands (Cumming *et al.* 2000; Takahashi *et al.* 2001; Pham *et al.* 2004) (Table 2.2), highlighting a reciprocal replacement pattern in canopy gaps for coniferous forests (Pham *et al.* 2004). In aspen dominated forests, gaps are usually large, created by largely trembling aspen tree mortality, and are usually filled by trembling aspen and other shade intolerant tree species (Cumming *et al.* 2000). In mixedwood forests (dominated by birch and spruce), spruce can establish itself under the shading of overstory trees, and will grow up into the canopy when space is made available (Takahashi *et al.* 2001). As well, fir appears to grow well in the shaded conditions created by a mixed fir and birch canopy (Mori and Takeda 2004). Although the canopy is closed, the increased light levels in northern microsites create conditions suitable for fir regeneration (Mori and Takeda 2004).

Table 2.2. Gap makers and gap fillers in different boreal stand types.

Stand type	Gap makers	Gap fillers
Trembling aspen dominated	Trembling aspen, balsam poplar	Trembling aspen, balsam poplar, paper birch
Balsam fir dominated	Balsam fir, paper birch, white spruce, black spruce	Balsam fir
Black spruce dominated	Balsam fir, paper birch, white spruce, black spruce	Black spruce
Birch and spruce mixedwood	Birch	Spruce and birch
Aspen and spruce mixedwood	Aspen	Spruce, balsam fir, and birch
Balsam fir and black spruce dominated	Balsam fir and black spruce	Balsam fir and black spruce

Birch regeneration on the other hand has been reported as being clumped around canopy birch trees (Takahashi *et al.* 2001). This is common for birch, which is known to regenerate by seed after fire, while maintaining itself by sprouting in the absence of fire (Takahashi *et al.* 2001). In coniferous forests, due to the small and infrequent nature of gaps (Bartemucci *et al.* 2002; Pham *et al.* 2004) and the limited germination sites that are suitable for shade intolerant broadleaf tree establishment, regeneration is largely restricted to shade tolerant conifers that can establish under the canopy of other trees where light is limited (Bartemucci *et al.* 2002).

It has been reported that in large gaps, the density of seedlings is higher in the shady southern portion of the gap than in the sunny northern portion of the gap in high latitude boreal forests (Coates 2002). Kneeshaw and Bergeron (1998) found that gap size increases and is more variable with forest age, driven by spruce budworm outbreaks that kill balsam fir and create gaps. Gaps allow for not only the regeneration of shade tolerant species such as balsam fir and eastern white cedar, but also for the maintenance of shade intolerant broadleaf species (Kneeshaw and Bergeron 1998). It is possible then that gap size may be controlling the species that can regenerate and the patterns of regeneration. However, after studying the influence of small gaps (<350 m^2) on understory regeneration and canopy transition probabilities of the trembling aspen forest in eastern Canada, Hill *et al.* (2005) reported that understory tree species composition and growth were independent of gap size and age, indicating that the relationship between overstory structure and understory regeneration founded in coniferous stands may not be applicable in broadleaf stands, where light availability is much higher (Chen 1997; Messier *et al.* 1999; Chen and Popadiouk 2002).

CWD Dynamics

There is less overall CWD in broadleaf old-growth forests than coniferous old-growth forests (Harmon and Hua 1991; Stewart *et al.* 2003). However, in mature, intermediate-aged boreal forests, the opposite trend has been found, in which mixedwood stands were discovered to have a greater amount of CWD than broadleaf stands, which in turn had more CWD than coniferous stands (Pedlar *et al.* 2002). Little information has been unearthed that contrasts CWD dynamics in different stand types for young forests. The distribution of CWD among size classes is similar for mixedwood and broadleaf forest types, while coniferous forests differ in that they lack CWD in large size classes (Pedlar *et al.* 2002). In mixedwood, broadleaf, and coniferous forests, the majority of CWD is in the form of DWD, followed by snags and then stumps (Siitonen *et al.* 2000; Pedlar *et al.* 2002; Stewart *et al.* 2003).

Snags

The BA of snags in old boreal forests has been found to be higher in coniferous forests than broadleaf forests (Stewart *et al.* 2003). No research, however, has compared the BA of snags among conifer, mixedwood, and broadleaf young and intermediate-aged boreal forest stands. The volume of snags is likely to be greater in coniferous forests than in broadleaf forests because broadleaf species generally have faster decomposition rates of snags than coniferous species do (Yatskov *et al.* 2003). This was confirmed by Stewart *et al.* (2003) who found that the volume of snags was higher in old coniferous forests than old broadleaf forests. However, little information is available comparing young and intermediate-aged conifer, mixedwood, and broadleaf stands.

The diameter distribution appears to change with time for both coniferous and broadleaf stands. In young broadleaf stands, the diameter distribution of snags is a reverse-J shape. However in old broadleaf stands, snags become present in larger diameter classes and the distribution of snags becomes more evenly spread out among the diameter classes as the reverse-J distribution becomes less and less prominent (Lee 1998). In contrast, the diameter distribution of snags in old coniferous stands has been shown to follow a reverse-J distribution with many smaller individuals and fewer larger ones (Kuuluvainen *et al.* 1998).

DWD

While no studies have been found that compare the volume of young and intermediate-aged coniferous and broadleaf forests with respect to DWD volume, the volume of DWD has been reported to be higher in old coniferous boreal forests than in old broadleaf boreal forests (Stewart *et al.* 2003). However, Hély *et al.* (2000b) found a contrasting trend, where old boreal mixedwood stands had the highest volume of DWD followed by broadleaf stands and then coniferous stands. Snag falldown rates for broadleaf forests are lower than those for coniferous forests, suggesting that broadleaf forests may contain a greater volume of DWD (Lee 1998). However, broadleaf species generally have faster decomposition rates of DWD than coniferous species (Yatskov *et al.* 2003), indicating that DWD may persist for longer on the forest floor in coniferous forests.

The size and density, projected ground cover, and total mass of DWD has been found to be significantly higher in coniferous forests than broadleaf forests (Harmon and Hua 1991). However, this study did not compare forests in similar geographic regions, and the differences between stand types may be highly confounded with the differences in site characteristics.

THE ROLE OF NON-STAND-REPLACING DISTURBANCES IN ALTERING STAND STRUCTURE

While fire is the major stand renewing disturbance mechanism controlling species distributions and assemblages in the boreal forest (Amiro *et al.* 2001), the importance of other disturbances in shaping forest structure is also evident (Blais 1981; Bergeron *et al.* 1995; D'Aoust *et al.* 2004; Bouchard *et al.* 2005). Non-stand-replacing disturbances help to maintain a heterogeneous forest structure (Antos and Parish 2002). In this section, the effects of these disturbances on forest structure will be explored.

Small-scale disturbances generate conditions for new trees to establish (De Grandpré *et al.* 2000), and for suppressed trees to be released into the canopy (Antos and Parish 2002). As boreal successional trajectories lead to a change from broadleaf dominance to coniferous dominance without disturbances (Bergeron and Dubuc 1989; Bergeron 2000; Gauthier *et al.* 2000; Harper *et al.* 2002), non-stand-replacing disturbances are essential to maintain the broadleaf component in forests, and can often lead to the maintenance of mixedwood stands for a very long period of time (Harper *et al.* 2002). Due to the extensive amount of non-stand-replacing disturbances that can affect forest structure in the boreal forest, this chapter will focus on wind-caused and insect-caused damage (exclusively the spruce budworm) and their effects on stand structure.

Wind

Extremely windy conditions can damage forests in a phenomenon called blowdown or windthrow. Wind can damage trees by uprooting them, snapping their trunks, or causing bending to occur (Webb 1988), resulting in blowdown, which largely affects the dominant canopy trees in a forest stand by blowing them to the ground (Kuuluvainen and Juntunen 1998; Kulakowski and Veblen 2003). In this way, blowdown is an important mechanism to allow a continuous supply of CWD to forest ecosystems (Huggard *et al.* 1999). Trees that are the colonizing cohort and usually early successional are most susceptible to blowdown (Kuuluvainen and Juntunen 1998). Following blowdown, canopy space is made available for suppressed, later successional species to grow up into the canopy from the subcanopy (Kulakowski and Veblen 2003). As well, blowdown can create microsites for new seedlings to establish by removing canopy closure and allowing light to penetrate to the forest floor, by creating a substantial amount of DWD, and by raising substrate and exposing mineral soil, making sites drier and reducing competition by creating sites largely free of herbaceous vegetation (Kuuluvainen and Juntunen 1998; Kulakowski and Veblen 2003). Both early successional trees (Kuuluvainen and Juntunen 1998) and late successional trees (Kulakowski and Veblen 2003) have been shown to recruit in openings created following blowdown.

Many species in the boreal forest (including spruce and fir) have a tendency to be uprooted instead of breaking at the bole (Webb 1988; Kulakowski and Veblen 2003), creating ideal regeneration conditions (Kulakowski and Veblen 2003). True firs also appear to be less susceptible to blowdown than spruce (Huggard *et al.* 1999). In contrast, other species such as trembling aspen have a tendency to be snapped, breaking at the bole (Webb 1988). Aspen dominated forests have been reported to have lower levels of blowdown (due to flexible stems with reduced wind drag), while spruce/fir forests have been shown to have higher levels of blowdown (as a result of denser tree canopies and shallower root systems) (Baker *et al.* 2002). Blown over trees have been found to have higher height/diameter ratios, attributed to trees with smaller diameters being more likely to be blow over than thicker trees (Cremer *et al.* 1982; Wonn and O'Hara 2001), whereas Huggard *et al.* (1999) have reported that wind-thrown trees had lower height/diameter ratios in a partial harvesting experiment. Huggard *et al.* (1999) suggests that topography may be confounding blowdown susceptibility in their study, which might help to explain their contradictory findings. Trees growing in rocky, exposed topography may be exposed to higher wind speeds and have lower height/diameter ratios. Further, lower levels of blowdown occur in stands with lower tree densities (Baker *et al.* 2002). While the effects of forest harvesting on stand structure will be discussed in a later section, it is important to note that harvesting can lead to an increase in blowdown (Huggard *et al.* 1999).

Spruce Budworm

Spruce budworm is a significant insect pest in the boreal forest from an economical perspective, affecting millions of hectares of forests and resulting in major losses of merchantable timber (MacLean and MacKinnon 1997). Outbreaks of spruce budworm can shape the forest structure substantially on sites dominated by tree species including balsam fir, white spruce, red spruce (*Picea rubens* Sarg.), black spruce, and the red-black spruce hybrid in the east (Morin 1994; MacLean and MacKinnon 1997; Bergeron and Leduc 1998; Bouchard *et al.* 2005) and subalpine fir and the white spruce/Engelmann spruce complex in the west (Antos and Parish 2002). Spruce budworm infestations weaken and defoliate balsam fir trees and create conditions where forest trees are more susceptible to being blown over (Morin 1994). If large older trees survive the insect attack and subsequent blowdown, then the forest may have a more uneven structure (Morin 1994). An outbreak that occurs over a number of years can lead to high tree mortality (Kneeshaw and Bergeron 1999) and CWD inputs into the overall CWD pool that lag slightly behind the actual timing of the outbreak (Fraver *et al.* 2002).

Outbreaks of spruce budworm are an important mechanism in creating canopy gaps in both subalpine (Antos and Parish 2002) and boreal (Kneeshaw and Bergeron 1999; Harper *et al.* 2002; D'Aoust *et al.* 2004) mixedwood and coniferous forests. The patches of open canopy created allow for the release of suppressed individuals into the canopy (Morin 1994; Antos and Parish 2002), and promotes growth into the overstory (Morin 1994). Spruce and fir prefer regenerating in the southern part of gaps while trembling aspen prefers the northern part, likely due to the increased levels of light (Kneeshaw and Bergeron 1999). The gaps created by spruce budworm outbreaks may be essential for the persistence of shade intolerant species such as trembling aspen in the landscape in areas where the fire cycle is long (Baskerville 1975). In contrast, shade tolerant species such as eastern white cedar, white spruce and balsam fir may prefer the southern part of the gap due to their preference for shade and higher moisture levels (Kneeshaw and Bergeron 1999).

Stand type plays a role in the extent of spruce budworm mortality and the impact on stand structure. In balsam fir dominated forests, spruce budworm outbreaks can be stand-replacing (Bouchard *et al.* 2005), creating a unimodal or bimodal structure (depending on the severity and duration of the outbreak) (Morin 1994). In balsam fir dominated forests, an increase in spruce budworm outbreaks occurs as TSF increases, attributed to an increase in the proportion of host coniferous species that make up the stand as succession proceeds (Bergeron and Leduc 1998; Harper *et al.* 2002; D'Aoust *et al.* 2004). These outbreaks lead to tree mortality in host species and are reflected as changes in canopy openness (D'Aoust *et al.* 2004). In contrast, mixedwood stands have been observed to have lower mortality levels than coniferous stands (Su *et al.* 1996; Bouchard *et al.* 2005). In these stands the development of a multi-level canopy structure is common (Bouchard *et al.* 2005).

Stands dominated by broadleaf trees (because they contain a low proportion of host species), show little change in canopy openness following spruce budworm outbreaks, while coniferous stands show a significant increase in canopy openness following an attack, with mixedwood stands being intermediate (D'Aoust *et al.* 2004). In contrast, Blais (1981) reported that budworm-induced mortality for white spruce and balsam fir trees are approximately the same in coniferous and mixedwood forests. Bergeron *et al.* (1995), however, found that the mortality rates of balsam fir were higher in coniferous stands than broadleaf stands with mixedwood stands being intermediate. The lower mortality rates of balsam fir stems in broadleaf stands may be related to overstory broadleaf trees creating situations where female spruce budworms experience difficulty finding subcanopy or understory balsam fir (Bergeron *et al.* 1995).

Outbreaks result in an increase in canopy gaps and influence gap distribution, depending on spatial arrangement of susceptible trees in a stand. D'Aoust *et al.* (2004) reported that before outbreaks, gaps are relatively uniformly distributed, whereas after an outbreak, gaps become patchy and heterogeneous in distribution, and gap size increases with an increase in the coniferous component. Spruce budworm outbreaks often have detrimental effects on the white spruce component of a stand, as the forest environment following a spruce budworm outbreak does not encourage white spruce regeneration (Bergeron and Dubuc 1989). A severe spruce budworm outbreak can result in mortality levels of approximately 90% for balsam fir and 50% for white spruce (Blais 1981), and it is possible that severe outbreaks can lengthen the interval between outbreaks due to the high mortality of balsam fir and white spruce that severe outbreaks cause (Blais 1981).

Mortality levels appear to differ with tree sizes and site condition. Bergeron *et al.* (1995) reported that balsam fir tree mortality (number of stems killed per unit area) increases as (1) the diameter of trees increases (indicating that smaller trees suffer less mortality than larger trees), (2) the percentage of coniferous stands that dominate the forest landscape increases, (3) stand age increases, and (4) balsam fir BA and abundance increases. While Bergeron *et al.* (1995) revealed that abiotic factors did not significantly affect balsam fir mortality rates caused by spruce budworm, MacLean and MacKinnon (1997) reported that defoliation by spruce budworm was higher on well-drained, more productive sites than less well-drained sites, possibly due to variation in egg-laying behavior of the spruce budworm females and higher foliage nutrient levels on richer sites. In contrast, Bouchard *et al.* (2005) found that balsam fir dominated stands suffered the greatest mortality on imperfectly drained soils.

Although spruce budworm outbreaks last longer in western Canada, they usually cause less mortality (Timoney 2003). Mortality levels have been directly related to the fire cycle, as mortality of balsam fir has been shown to increase with an increase in fire cycle, likely due to an increase in overall balsam fir abundance in the stands (Bergeron and Leduc 1998). Therefore, it is likely that in areas where climate change leads to a longer fire cycle, spruce budworm-induced mortality will increase, while areas that experience a shorter fire cycle will have a decrease in spruce budworm-induced mortality (Bergeron and Leduc 1998). In particular, spruce budworm outbreaks may be responsible for maintaining mixedwood stands in areas of the boreal forest with longer fire cycles (Kneeshaw and Bergeron 1999).

THE IMPACT OF CLIMATE AND GEOGRAPHY ON BOREAL STAND STRUCTURE

Due to its circumpolar distribution and extensive geographic range, the boreal forest is subject to highly variable climatic conditions from one region to the next (Weber and Stocks 1998; Amiro *et al.* 2001). The dynamics of a stand are impacted substantially by climatic conditions, as climate plays an important role in determining fire regimes (Overpeck *et al.* 1990; Bergeron 1991; Suffling 1995; Lesieur *et al.* 2002), tree species and other vegetation distributions (Bonan *et al.* 1992; Hogg 1994; Suffling 1995; Flannigan and Bergeron 1998), and successional pathways (Overpeck *et al.* 1990; Chen and Popadiouk 2002). In this section, I will discuss (1) how fire cycle varies regionally and how fire cycle and geography impact structure, (2) how the fire cycle has changed since the termination of the Little Ice Age, (3) how climate change is projected to affect the fire cycle and how this might impact structural dynamics, species distributions and wildlife, (4) and the implications of climate change on the earth's carbon balance.

Geography and Fire Cycle and their Influence on Species and Structural Dynamics

In the Canadian boreal forest, the fire cycle decreases from Newfoundland in the east to Alberta in the west (Johnson 1992; Suffling 1995; Bergeron *et al.* 2001). This decrease in fire cycle from east to west can be attributed to many factors including probability of lightning strikes and climate, both of which affect the fire weather and the fire regime (Bergeron *et al.* 2001; Kneeshaw and Gauthier 2003). The westcentral portion of the country is characterized as having relatively dry and severe fire weather which contributes to the high incidence of fires (Amiro *et al.* 2001; Kneeshaw and Gauthier 2003).

In areas where the fire frequency, i.e., "the number of fires per unit area per year" (Bergeron 1991) is high, frequent fires can result in cyclic succession maintaining intolerant colonizing species as the dominant tree species until the next fire (Dix and Swan 1971; Carleton and Maycock 1978; Johnson 1992), whereas long fire cycles can produce directional succession, leading to species replacement of shade intolerant tree species by shade tolerant ones (Bergeron *et al.* 2001; Lesieur *et al.* 2002). With long fire cycles, the importance of secondary disturbances such as insects, disease, and blowdown with respect to shaping forest structure increases in importance (Bergeron and Leduc 1998; Bergeron *et al.* 2001). The fire regime is also responsible for controlling species distributions (Bergeron and Brisson 1990; Flannigan and Bergeron 1998; He *et al.* 2002). For example, the fire regime appears to limit the northward distribution of red pine due to the higher intensity of fires that occurs in the northern boreal forest compared to the south (Bergeron and Brisson 1990; Flannigan and Bergeron 1998), although highly frequent fires of low intensity promote red pine abundance (Engstrom and Mann 1991).

Disturbance regime, climatic conditions, successional stage, activity of decomposing organisms, composition of tree species, and soil productivity are largely responsible for determining the amount of CWD in a stand (Linder *et al.* 1997). Moist sites generally have higher volumes of CWD than drier sites (Feller 2003). This is likely due to higher productivity (more tree biomass production) on moist sites, but may also be a consequence of longer fire cycles that generate larger pre-disturbance production of CWD or by slower DWD decomposition (Spies *et al.* 1988; Feller 2003). This is supported by Sippola *et al.* (1998), who found that productive sites have higher living and dead timber volumes than less productive sites. In contrast, it has been suggested that areas with less precipitation and colder temperatures have slower microbial activity and reduced decomposition rates (Harmon and Hua 1991; Hély *et al.* 2000a), resulting in a build-up of DWD on the forest floor (Hély *et al.* 2000a).

Northern boreal forests have been found to be structurally different from southern boreal forests (Fridman and Walheim 2000; Siitonen *et al.* 2000; Rouvinen *et al.* 2002). Old-growth forests in Fennoscandia and Russia were reported to contain higher CWD volumes in hemiboreal and southern boreal regions than northern boreal regions (Siitonen *et al.* 2000). In contrast, Fridman and Walheim (2000) and Rouvinen *et al.* (2002) reported that the volume of CWD increases from the south to the north, attributed to a harsher climate in the northern areas that favour slower decomposition rates and added CWD accumulation. The contrasting results of these studies may be attributed to differences in study regions, stand type, or site type. Nilsson *et al.* (2002) reported that the density of large, living trees in northwestern North American old-growth boreal forests is several times higher than that in other boreal regions in Europe and North America.

Changes in the Fire Cycle since the Little Ice Age

North American boreal forests have holistically experienced an increase in fire cycle since the end of the Little Ice Age (approximately 1850 AD) (Clark 1988; Flannigan *et al.* 1998; Bergeron *et al.* 2001; Lesieur *et al.* 2002), where the number of fires and area per year that is burned has decreased since about 1850 to present (Bergeron 1991; Bergeron *et al.* 2001). This temporal change in fire cycle and the variation in fire cycle among regions is likely driven by climate rather than by direct human involvement (including suppression) (Flannigan *et al.* 1998; Bergeron *et al.* 2001; Lesieur *et al.* 2002). This is supported by Timoney (2003) who concluded that fire suppression has had little effect on decreasing the annual area burned in the prairies of western Canada. However, Linder *et al.* (1997) and Linder (1998) found that fire suppression has been effective in significantly altering the natural forest structure in some areas of the boreal forest by almost completely eliminating fires, thereby reducing the heterogeneous nature of the landscape. By suppressing fire, old-growth conditions created may increase the likelihood of larger, more detrimental fires in the future (Hendrickson 2003).

The Potential Impacts of Climate Change on the Disturbance Regime and Forest Stand Structure

A changing climate has the potential to impact species distributions. It is predicted that higher carbon dioxide (CO_2) levels will continue to bring about an increase in the earth's temperature (Stocks *et al.* 1998). With an increase in CO_2 and resulting warmer temperatures, species distribution will change, as some species will advance northward (Bonan *et al.* 1992; Suffling 1995; Thompson *et al.* 1998; He *et al.* 2002). However, for other species a northward movement will be difficult due to changes in abiotic conditions, such as soil properties, that will hinder advancement (Suffling 1995).

Bonan *et al.* (1992) suggests that climatic warming may initiate a positive feedback response where a warmer climate would cause the northward migration of the boreal forest, which would in turn result in further warming. While boreal species may move northward, it is likely that southern tree species will move northward into the current boreal range (He *et al.* 2002). The consequence of this within the current boreal forest range may be a decrease in abundance of northern temperate broadleaf and boreal tree species (Suffling 1995; He *et al.* 2002), and an increase in the abundance of more southern temperate species such as white ash (*Fraxinus americana* L.), bur oak (*Quercus macrocarpa* Michx.), black oak (*Quercus velutina* Lam.) and white oak (*Quercus alba* L.) (He *et al.* 2002) and fire avoiders such as white spruce and balsam fir (Suffling 1995; Flannigan *et al.* 1998). However, Overpeck *et al.* (1990) predicted a greater proportion of the landscape being occupied by early successional species in the boreal as the consequence of global warming.

In the western boreal and temperate forests, predicted climatic warming will likely alter disturbance regimes, leading to less precipitation and an increase in fire frequency and intensity, which has the potential to cause a homogenization of the forest landscape with reduced diversity and complexity and leading to the decline of some forest tree species (Clark 1988; Overpeck *et al.* 1990; Thompson *et al.* 1998; Amiro *et al.* 2001). If general circulation models (GCM) hold true (Stocks *et al.* 1998), North American boreal forests will be more subject to fire danger, especially in the westcentral portion (Stocks *et al.* 1998), where large portions of the boreal landscape may be transformed into grassland and early successional forests (Flannigan *et al.* 1998; Amiro *et al.* 2001), resulting in loss of forest cover and forest fragmentation (Hogg 1994; He *et al.* 2002). However, higher temperatures do not necessarily indicate that fire disturbances will be larger and more frequent (Bergeron and Flannigan 1995; Flannigan *et al.* 1998). In the eastern portion of the boreal forest, it is predicted that the fire cycle will continue to increase under projected warming trends (Bergeron and Flannigan 1995; Flannigan *et al.* 1998; Bergeron *et al.* 2004). This decrease is driven by the precipitation regime of the region, which is quite different from that in the west (Bergeron and Flannigan 1995; Bergeron *et al.* 2004).

Climate Change and Carbon Ecosystem Stores

The processes that influence and are influenced by CWD are essential in managing carbon retention in boreal forest ecosystems (Yatskov *et al.* 2003). The input of CO_2 to the atmosphere as a consequence of CO_2 flux from CWD and CO_2 soil surface flux appears to be important in fire-prone boreal forests (Krankina and Harmon 1995; Mäkipää *et al.* 1999; Wang *et al.* 2002; Wang *et al.* 2003). Soil surface CO_2 fluxes increase with increasing soil temperature and broadleaf forest component while decreasing with increasing forest stand age (Mäkipää *et al.* 1999; Wang *et al.* 2003). As well, CWD CO_2 flux increases as the temperature of air and CWD rises (Wang *et al.* 2002). However, under warmer climatic conditions, it is predicted that the carbon stores in vegetation will increase as net primary productivity increases (Mäkipää *et al.* 1999), which may offset some of the releases of carbon by soil surface and CWD CO_2 flux.

At the stand level, younger stands have the potential to sequester more carbon annually than older stands because of their higher production rates (i.e., photosynthetic rates) (Goulden *et al.* 1998). However, at the landscape level, it is likely that an increase in fire frequency in some areas of the boreal forest, as a consequence of global warming, may lead to an increase in overall CO_2 flux to the atmosphere and an increase in the percentage of young forests on the landscape (Krankina and Harmon 1995; Thompson *et al.* 1998; Mäkipää *et al.* 1999; Amiro *et al.* 2001). The increase in CO_2 emissions may in turn bring about a positive feedback where higher rates of CO_2 emissions cause more fires and greater CO_2 emissions (Amiro *et al.* 2002). Consequently, it is possible that the boreal forest may turn from an important carbon sink into a carbon source (Mäkipää *et al.* 1999; Amiro *et al.* 2001). However, in some areas of the boreal forest, longer fire cycles may accompany the warmer temperatures (Bergeron and Flannigan 1995; Flannigan *et al.* 1998), and under these conditions, the slower rates of decomposition in older forests and reduced releases of carbon through combustion (due to less fires) (Wardle *et al.* 2003) may cause the boreal forest to continue to be a carbon sink (Flannigan *et al.* 1998; Wardle *et al.* 2003). This highlights the complexities surrounding this issue and stresses the need for further investigation.

A COMPARISON OF STAND STRUCTURE IN NATURAL AND MANAGED BOREAL FORESTS

Clearcut logging (hereafter referred as clearcutting) is the most common harvesting method used in many areas of the boreal forest. The use of clearcutting to emulate the conditions created by natural disturbances is at best well-intentioned naïveté but in reality is a misleading interpretation of many known ecological processes (Keenan and Kimmins 1993; McRae *et al.* 2001). While both clearcutting and fire remove the tree canopy and bring about changes in ground microclimate (Keenan and Kimmins 1993; Carleton and MacLellan 1994), it appears that CWD dynamics of burned stands are different from that of clearcut stands (Brumelis and Carleton 1988; Linder and Östlund 1998; Sippola *et al.* 1998; Krankina *et al.* 2002). Forest fires are responsible for creating new dead organic material by killing the stems of trees, burning root systems and scorching crowns (Sippola *et al.* 1998). These dead trees remain as snags for a variable length of time before eventually falling to the forest floor (Sippola *et al.* 1998). In contrast, clearcutting removes organic material from the forest, and results in a disruption in the production and availability of CWD for a substantial length of time (Sippola *et al.* 1998).

For the remainder of this section, "natural stands" will refer to stands that were disturbed by a stand-replacing fire, whereas "managed stands" will refer to stands that have undergone harvesting activities such as clearcutting, selective cutting and thinning. While studies have explored the differences between natural and managed stand structure (Pedlar *et al.* 2002; Rouvinen *et al.* 2002; Storaunet and Rolstad 2002; Ruel *et al.* 2004), a study that characterizes the differences between the living tree and CWD dynamics of natural and managed stands along a chronosequence with similar abiotic conditions is needed for better understanding of long-term impacts of clearcutting on forest stand structure. Because of this, an accurate comparison of stand structural dynamics in fire-origin stands versus clearcut-origin stands is difficult. This section will investigate the dynamics of CWD and living trees in natural and managed boreal forest stands. It will also outline the impacts of clearcutting and selective cutting on biodiversity with special reference to old-growth forests.

Living Tree Dynamics

Forests that are logged differ considerably from natural forests with respect to some of their live tree characteristics (Brumelis and Carleton 1988; Linder and Östlund 1998; Rouvinen *et al.* 2002; Ruel *et al.* 2004), while other characteristics appear to be similar (Reich *et al.* 2001). It has been reported that the volumes of live trees, numbers of large living trees, and broadleaf tree component is lower while the density of live trees is higher in logged stands compared with natural stands in the old-growth state (even though a considerable length of time had passed since logging occurred) (Linder and Östlund 1998; Rouvinen *et al.* 2002; Ruel *et al.* 2004). However, Reich *et al.* (2001) found that the BA of trees in young and old post-fire stands was similar to those post-logged, indicating that stand origin has no significant effect on the BA of trees in a stand in the southern boreal forest. Ferguson and Elkie (2003) found that the density of live trees was lower in young managed stands when compared to young natural stands, with no significant differences in BA between the two. This was supported by Brumelis and Carleton (1988) who also found that the density of live trees was higher in natural stands compared with clearcut stands in black spruce dominated forest. As well, tree height has been found to be lower in younger logged black spruce stands compared with burned black spruce stands (Ruel *et al.* 2004). This is possibly due to trees in logged stands having to acclimate to new growing conditions or because of lower nutrient levels (Ruel *et al.* 2004). However, the difference in height between logged and natural stands faded after the stands reached an age of approximately 50 years (Ruel *et al.* 2004). Further, Ruel *et al.* (2004) also found that black spruce in logged stands allocated more biomass to the development of branches and leaves than to their stems, but it is unclear why different stand origins resulted in different allocation patterns.

Logging can lead to a temporary nutrient flush, and as broadleaf trees generally have a competitive advantage over conifers on nutrient-rich sites, the composition of species may change in favour of an increased broadleaf component at the expense of conifers after disturbance (Brumelis and Carleton 1988; Carleton and MacLellan 1994). Coniferous regeneration may also be poorer on logged sites than natural sites due to a greater abundance of ericaceous shrubs on logged sites that hinders coniferous growth (Ruel *et al.* 2004). As well, seedling recruitment is poor in the large open areas created by clearcuts, except for shade intolerant broadleaf trees such as trembling aspen (Coates 2002). Logging also has been shown to destroy advanced regeneration, which may also be hindering coniferous regeneration in logged areas (Ruel *et al.* 2004).

The spatial configuration of live trees is different in areas that are burned, as compared to areas that are clearcut (Niemelä 1999). Fire burns in a heterogeneous fashion and leaves patches of unburned trees on the landscape. In contrast, clearcutting removes most of the trees from harvested areas (Niemelä 1999). However, guidelines have been written in an attempt to promote live tree retention during harvesting operations (Ontario Ministry of Natural Resources 2001). There is little information available that compares live tree characteristics along a chronosequence for stands that are harvested versus burned and allowed to develop without additional human intervention such as partial or selective cutting and thinning. The need for this kind of study is crucial if forest management decisions are going to be made that more effectively reflect the natural stand structure of boreal forest ecosystems.

CWD Dynamics

Following clearcutting, less residual material is left behind than what is left following a natural disturbance (Fleming and Freedman 1998; Krankina *et al.* 2002; Pedlar *et al.* 2002). In young forests, CWD volume, snag abundance, snag BA, and volume of large snags and DWD is significantly higher in natural stands than in clearcut stands (Fridman and Walheim 2000; Krankina *et al.* 2002; Pedlar *et al.* 2002). While the volume of DWD is similar, the snags that contribute a large proportion of CWD in natural stands are largely absent in managed stands shortly after disturbance (Pedlar *et al.* 2002), as stand-replacing fire leaves many large snags (killed during the fire) while clearcutting does not (Pedlar *et al.* 2002; Rouvinen *et al.* 2002). Instead, clearcutting produces small logging slash in early states of decay that breaks down quickly (Fraver *et al.* 2002). The distribution of CWD in natural forests has been found to be fairly even among small, medium, and large classes, whereas the CWD in managed stands has been found to be largely skewed towards small diameter classes (Fridman and Walheim 2000; Fraver *et al.* 2002; Pedlar *et al.* 2002). Even in intermediate-aged and old forests, the volume of CWD appears to be higher in natural forests than forests where the stand-initiating disturbance was clearcutting (Krankina *et al.* 2002). Therefore, managed stands differ remarkably from natural stands in the amount, type, and size of CWD that is produced (Fridman and Walheim 2000; Pedlar *et al.* 2002; Rouvinen *et al.* 2002), and the ability of clearcutting to effectively emulate the forest structure of burned stands is seriously questionable.

Both timber harvesting and fire create forest edge that fragments the boreal forest, but unlike fire, clearcuts create forest edges that are narrower, have less snags, a less extensive structural change, an increase in tree mortality and snag breakage, and a sudden edge-to-interior forest transitional gradient (Harper *et al.* 2004). It is therefore evident that forest edge created by clearcut harvesting does not mimic the edge created by fire, and because of this, clearcut edge may not be able to fulfill the necessary habitat requirements for some species that rely on forest edge created by fire (Harper *et al.* 2004). Selective cutting and thinning also have significant impacts on forest structure. These activities lower the overall CWD volume, decrease the number of large DWD and snags, diminish the overall snag abundance, and increase the decomposition rates while decreasing landscape heterogeneity and the unevenness of a stand (Kolström 1998; Siitonen *et al.* 2000; Jantunen *et al.* 2002; Storaunet and Rolstad 2002).

The Impacts of Timber Harvesting on Biodiversity

In recent years, the effect of harvesting on biodiversity and ecosystem sustainability has been closely scrutinized. Maintaining biodiversity has many benefits, including the ability to buffer ecosystems against unforeseen perturbations (Niemelä 1999). Biodiversity in the boreal forest may be maintained by mechanisms that create secondary succession at both small and large scales such as forest fires and gap phase dynamics, that can affect a few square meters (e.g. death of a single tree) or several thousand hectares (e.g. forest fire) (Niemelä 1999).

Wildlife can be severely affected by harvesting activities, and in many areas, intensive logging has resulted in the loss or decline of forest species including Gapper's red-backed vole (*Clethrionomys gapperi* Vigors) (Moses and Boutin 2001) and the woodland caribou (*Rangifer tarandus caribou* Gmelin) (Chubbs *et al.* 1993). The American marten (*Martes americana* Turton) appears to prefer sites with diverse stand structure including tall trees, a high density of tall snags, large diameter DWD, a high BA of broadleaf trees, and a suitable subnivean habitat to forage for small animals (Sturtevant *et al.* 1997; Payer and Harrison 2003). Harvesting usually occurs at an age that corresponds to the lowest volumes of CWD in stands (Sturtevant *et al.* 1997), and consequently, the lower volumes of CWD that remains following harvesting may be detrimental to marten populations by limiting habitat availability (Payer and Harrison 2003). Further, managed forests contain less large diameter snags and trees, which has the potential to negatively impact many cavity dwelling animals, cavity nesting birds, and large raptors (Linder and Östlund 1998; Imbeau *et al.* 1999; Delong and Kessler 2000).

It has been suggested that alternative forest harvesting techniques can be used in an attempt to lessen the impact of forest harvesting. Asselin *et al.* (2001) suggests using strip clearcutting and seed-tree systems to help in the effective regeneration of some coniferous species such as white spruce and eastern white cedar, when clearcutting would create situations where seeds banks are far away. Moses and Boutin (2001) in turn suggest that implementing live tree patch retention can lessen the negative impacts on some small mammal populations. As well, alternative harvesting methods such as 'harvesting with advance regeneration protection' (HARP) can be used to increase the retention and redevelopment of old-growth features more effectively than traditional harvesting methods (clearcutting) in the boreal forest (Deans *et al.* 2003). Finally, with the increase in fire cycle that is expected to occur in some areas of the boreal forest (Flannigan *et al.* 1998; Bergeron *et al.* 2004), the use of clearcutting may not be appropriate for all areas. As such, Bergeron (2004) recommends clearcutting some areas (followed by seeding or planting), partially cutting other areas (to resemble overmature forests), and using selective cutting in still others (to retain old-growth characteristics) in an attempt to emulate a heterogeneous forest structure at the landscape level.

While harvesting is the most significant anthropogenic disturbance mechanism in the boreal forest, other human activities such as farming and the oil and gas industry (especially in the western boreal) are continuing to expand and further fragment the landscape, contributing more and more to habitat loss and degradation (Timoney 2003), which will likely put additional pressure on boreal species. Further, harvested sites are occasionally planted with tree species that are different from the ones that used to inhabit the site, thereby changing tree species assemblages and impacting biodiversity (Timoney 2003).

The Impacts of Timber Harvesting on Old-Growth Forest Structure

The characteristics that define boreal forest old-growth state are still widely debated and with the public's concern over the perceived decline in old-growth forest (Mosseler *et al.* 2003), criteria must be established that can be used to identify old-growth boreal forest. In an attempt to develop structural criteria to identify old-growth forest, Lee *et al.* (2000), Nilsson *et al.* (2002), Kneeshaw and Gauthier (2003), Mosseler *et al.* (2003), and Zenner (2004) made the following generalizations regarding boreal forests that are in an old-growth state:

1. About 10% of all stems are dead.
2. The percentage of dead trees that are standing is between 20% and 40% of total CWD volume and BA.
3. High structural complexity exists.

4. An intricate combination of large, old trees and young, small trees can be found.
5. The cohort BA ratio (CBAR) is between 0.3-0.4. The CBAR increases (with a maximum value of 1 and a minimum value of 0) as TSF increases.

Old-growth forests provide a variety of ecosystem services including storing large amounts of carbon, habitat protection, preserving a reservoir of genetic diversity, and improving water quality (Frelich and Reich 2003; Mosseler *et al.* 2003). There is much concern in forestry today over the loss of old-growth forests, as the loss of these forests will influence the species that require them for forest habitat (Niemelä 1999). Numerous species of predatory arthropods, small and large mammals, fungi, birds, amphibians, reptiles, and vascular plants require forests with old-growth characteristics (Niemelä 1999; Delong and Kessler 2000; Edman and Jonsson 2001; Mosseler *et al.* 2003). Many of these species are endangered (Edman and Jonsson 2001), stressing the need for protection of existing old-growth forest and using forest management to promote the development of old-growth forest in the future.

The loss of old-growth forests from the landscape as a result of timber harvesting and other anthropogenic causes has the potential to impact the earth's CO_2 levels, as young and mature clearcut stands have lower deadwood carbon stores than old-growth forests (Krankina and Harmon 1995). Therefore, the loss of old-growth forests may cause an input of CO_2 to the atmosphere and influence climate change through global warming. Also, as forests age, they increase in reproductive fitness and genetic diversity, thereby serving as important gene pools (Mosseler *et al.* 2003). The loss of these older forests may be harmful from a genetic standpoint for boreal forest trees (Frelich and Reich 2003; Mosseler *et al.* 2003).

Following harvesting, the slowest component to recover in attaining natural structure is CWD, and therefore, management practices that try to emulate the structure of old-growth characteristics in forest management are desirable (Siitonen *et al.* 2000). While old-growth forests have traditionally been thought of as forests that have not been harvested (Hendrickson 2003), it is possible that second growth forests that have been harvested could in time develop to be old-growth forests (Mosseler *et al.* 2003). If young harvested stands have the same structure as young natural stands, then it is likely that provided the young harvested stand is allowed to develop without anthropogenic influences, it will develop to resemble a natural stand (Frelich and Reich 2003).

SUMMARY

1. Stand structure has important implications for forest ecosystems including the maintenance of wildlife habitat, sustaining and indicating biodiversity, nutrient cycling, regulating climate through carbon storage, and affecting forest regeneration.
2. Surficial deposits and landscape configuration are important contributors in determining which species will colonize which areas of forest and in influencing successional pathways.
3. Fire is the dominant stand-replacing disturbance in the North American boreal forest, as stand structure is largely a reflection of the time since last stand-replacing fire. Fire-origin stands are characterized as having a sigmoid accumulation pattern with stand age.
4. Research is lacking that compares and contrasts CWD and live tree dynamics in different stand types within similar environmental conditions and in mixedwood forests in general along the chronosequence.
5. Over time, a forest stand changes from having a largely even-structured canopy to developing a canopy that is heterogeneous and multi-layered in structure. As forests age, they develop larger CWD that is more evenly spread out among diameter and height

classes and decay states. However, following a stand-replacing fire, the production of large sized CWD can be significant. This CWD originates from the pre-disturbance stand (trees killed during the fire and CWD from the pre-disturbance stand that survives the fire).

6. Downed woody debris are important regeneration microsites for many species as well as being an important habitat requirement for wildlife. In turn, snags also have important wildlife value.
7. Non-stand-replacing disturbances such as blowdown and spruce budworm outbreaks play an important role in altering forest structure and maintaining a broadleaf component for many forests when TSF is long, by removing canopy trees, freeing up available growing space, reducing the coniferous component of dominating trees, and creating microsites for new trees to establish.
8. The Canadian boreal forest has a fire cycle that increases in general from the west to the east. The North American boreal forest is highly variable in climate across its geographic range, and it is still unclear how predicted climate change scenarios will affect tree species dynamics and distributions, the regional fire cycle, and overall carbon ecosystem stores. As a result, at the landscape level, the boreal forest may turn from a CO_2 sink into a CO_2 source.
9. Clearcutting is a common harvesting practice throughout the North American boreal forest. It has been employed under the assumption that it effectively emulates boreal natural disturbances, specifically a stand-replacing fire. However it appears that CWD characteristics are considerably different between fire- and clearcut-origin stands. Little study has been done to compare the stand structure of the two origins along a

chronosequence where both have been allowed to develop without further anthropogenic influences. If effective forest management decisions are going to be made, this type of study must be undertaken.

CHAPTER THREE VERTICAL STRUCTURAL DYNAMICS OF FIRE-ORIGIN BOREAL CONIFER, MIXEDWOOD, AND BROADLEAF STANDS IN CENTRAL CANADA

INTRODUCTION

Vertical stand structure attributes such as tree and snag stem volume, basal area (BA), and density have been linked to many ecosystem processes including providing wildlife habitat and maintaining biodiversity (MacArthur and MacArthur 1961; Willson 1974; Linder and Östlund 1998; McRae *et al.* 2001; Moses and Boutin 2001; Ecke *et al.* 2002; Payer and Harrison 2003) and storing carbon (Mäkipää *et al.* 1999; Amiro *et al.* 2001; Wardle *et al.* 2003). In the boreal forest, vertical stand structure changes over time from relatively homogeneous in the diameter and height of trees and snags to bimodal or multi-modal with a broad range of heights and diameters (Paré and Bergeron 1995; Linder *et al.* 1997; Kuuluvainen *et al.* 1998; Clark *et al.* 2003). Stand BA, volume, and biomass of trees increases through stand development, but decrease marginally in older stands (Paré and Bergeron 1995; Delong and Kessler 2000; Popadiouk *et al.* 2003; Wardle *et al.* 2004) while stand density decreases with time since fire (TSF) (Lee *et al.* 1997; Delong and Kessler 2000; Popadiouk *et al.* 2003). Stand snag volume, BA, and density follows a U-shaped distribution along the chronosequence (Lee *et al.* 1997; Clark *et al.* 1998; Lee 1998; Pedlar *et al.* 2002) as a consequence of tree death by stand-replacing fires, competition-induced mortality during self-thinning, and longevity-related mortality (Oliver and Larson 1996; Lee *et al.* 1997; Clark *et al.* 1998; Greif and Archibold 2000; Hély *et al.* 2000a; Chen and Popadiouk 2002).

Tree and snag volume, BA, and density have been found to differ with stand composition. Stewart *et al.* (2003) reported that volume, BA, and density of trees were lower in 178-214 year-old broadleaf stands compared to conifer stands in Nova Scotia, Canada. Edgar and Burk (2001) found that productivity measured by BA was correlated positively with the trembling aspen (*Populus tremuloides* Michx.) component and negatively with canopy vertical structure, indicating that pure trembling aspen and single-canopied stands were expected to be the most productive in northern Minnesota, USA. Exceptions were found, however; the two most productive stands were vertically stratified, trembling aspen - balsam fir (*Abies balsamea* L.) - paper birch (*Betula papyrifera* Marsh.) mixtures. In a study undertaken in northwestern Quebec, Canada, Hély *et al.* (2000b) reported that 117 year-old broadleaf stands had the highest stand BA of trees followed by 236 year-old conifer stands and 175-205 year-old mixedwood stands. However, the large range in stand ages among stand types in their study does not allow isolating the effect of stand composition on tree and snag volume, BA, and density.

Structural diversity of trees and snags, defined as their size variability (Staudhammer and Lemay 2001; Varga *et al.* 2005), is a relatively new concept in forest ecology, and has been sparingly investigated in the boreal forest. In a study in western Canada, Varga *et al.* (2005) found that tree-size diversity, a measure of variability of tree-size, was higher in mixed-species stands than in single-species stands. Further, tree-size diversity was reported to decrease or increase with TSF depending on stand type and site index. Snags provide valuable habitat for many species of birds and mammals (Raphael and White 1984; Newton 1994; Robb *et al.* 1996; McRae *et al.* 2001; Sedgeley 2001) and therefore have been included in my measure and evaluation of structural diversity.

The goal of this study was to further understanding of the vertical stand structural dynamics as affected by stand composition and stand development in the central region of the boreal mixedwood forest in Canada. On glacial tills in this region, both single- and mixed-species stands of broadleaf and conifers are common (Rowe 1972). At early stages of stand development, jack pine (*Pinus banksiana* Lamb.) and trembling aspen are dominant species. At later stages of development, dominant conifers include black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss, and balsam fir, while dominant broadleafs are paper birch. My specific objectives were to address (1) how tree and snag volume, BA, density, and structural diversity (measured using Shannon's index and coefficient of variation (CV)) change along a chronosequence and (2) whether these structural attributes differ with stand composition.

MATERIALS AND METHODS

Study Area

The study was conducted in the boreal forest north of Lake Superior and west of Lake Nipigon in a transition between the Superior (B.9) and the Upper English River (B.11) Forest Regions (Rowe 1972), approximately 150 km north of Thunder Bay, Ontario (48° 22' N, 89° 19' W, 199 m elevation). The study area has a moderately dry, cool climate with short summers. The average annual precipitation for Thunder Bay (1971-2000) is 712 mm and the average annual temperature is 2.5 °C (Environment Canada 2005). Topographic features were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago.

Rowe (1972) described the forest of the region as containing a mix of paper birch, trembling aspen, balsam fir, white spruce and black spruce, jack pine, eastern white cedar ((*Thuja occidentalis* L.), and tamarack (*Larix laricina* (Du Roi) K. Koch), with a small contribution on certain sites from red and white pine (*Pinus resinosa* Ait. and *Pinus strobus* L., respectively), yellow birch (*Betula alleghaniensis* Britt.), black ash (*Fraxinus nigra* Marsh.), and sugar maple (*Acer saccharum* Marsh.). The natural stand-initiating disturbance of the area is predominately stand-replacing fire, which is also the most common stand-replacing mechanism in the boreal forest (Johnson 1992).

Sampling Design

I studied three stand types: 1) conifer dominated by jack pine at earlier stages of development and a mixture of black spruce, white spruce, and balsam fir at later stand development, 2) broadleaf dominated by trembling aspen at earlier stages of development and paper birch at later stand development, and 3) mixedwood which consisted of a mixture of trembling aspen and jack pine in earlier stages of development and a mixture of black spruce, white spruce, balsam fir, and paper birch at later stages of development. Stands were selected using random stratified sampling along a chronosequence from stands of fire-origin with ages ranging from 72 to 201 years (Appendix I, II). The determination of stand type was based on a modification of methodology used by Greif and Archibold (2000). Stands were assessed as belonging to a specific stand type based on the density of conifer trees that dominated the overstory of the stand. Stands with greater than 75% conifer component were classified as "conifer type", stands with 25-75% conifer component were classified as "mixedwood type", and stands with less than 25% conifer component were classified as "broadleaf type".

The disturbance origin for each plot was determined through forest resource inventory information, silvicultural records, and provincial fire disturbance maps. Verification in the field was done by visually estimating CWD and tree density.

In order to limit soil variability, all stands were sampled on prevailing mesic, upland sites with a slope <10%. On each site, a soil pit was dug using methods outlined by British Columbia Ministry of Environment and British Columbia Ministry of Forests (1998) and assessment followed Sims *et al.* (1997) and Soil Classification Working Group (1998). For all sites, the soil order was Brunisol with sandy loam, sandy clay loam, or clay loam soil texture.

In total, 33 stands were sampled. Mixedwood stands of approximately 139 years of age were not available for sampling in the study area. This gap in mixedwood stand age is likely caused by the infrequency of fire in the study area which resulted in narrowed sampling possibilities.

Field Measurements

For each selected stand, I used tree ages to estimate TSF (Bergeron 1991). Of all the sampled stands, I was able to select either post-fire jack pine or trembling aspen trees for the determination of TSF. For each of the stands aged 72 to 139 year-old, no fewer than three canopy stems were sampled. For each selected tree, a core or disk at breast-height was taken and brought to the laboratory. In the laboratory, the cores mounted on constructed core strips and disks were transversely and sanded to make rings visible. Rings were then counted using a hand-held magnifier until the same count was obtained three successive times. Tree ages were corrected to TSF by adding seven years for trembling aspen and eight years for jack pine using the model developed by Vasiliauskas and Chen (2002). For the oldest burnt area, i.e., 201 year-old stands, one live jack pine tree and seven jack pine snags were sampled and disks were cut at the base of stems. The ring count of live tree was 201 years and that of snags ranged 140 to 180 years. I used the live tree age as TSF for the area.

Within each stand, a 400 m^2 circular plot was established to represent the stand. Within the plot, the diameter at breast-height (DBH) (approximately 1.3 m above the root collar) of all trees (DBH $\geq$10 cm, some living foliage) and snags (DBH $\geq$10 cm, height $\geq$2 m, <45° vertical lean, and no living foliage) was measured and recorded. Snag criteria were based on Lee *et al.*

(1997). While the heights of all snags were measured, I randomly sampled five trees from each 5-cm DBH class for each species and their heights were measured using a clinometer. These classes are as follows: (1) 10-14.9 cm, (2) 15-19.9 cm, (3) 20-24.5 cm, (4) 25-29.9 cm, and (5) ≥30 cm. Tree heights for the remaining trees were estimated using species-specific non-linear regression models developed from the paired height and DBH measurements. The height-DBH models were developed by fitting the Chapman-Richards function (eq. 1) as outlined by Peng *et al.* (2001):

$$[1] \qquad H = 1.3 + a(1 - e^{-b\,DBH})^{c}$$

where H is tree height (m), a is an asymptote parameter, b is a scale parameter, c is a shape parameter, and DBH is diameter at breast-height (cm) (Table 3.1). Tree and snag heights were divided into 4-m height classes (based on recommendations of Varga *et al.* (2005)) as follows: (1) 2-5.9 m, (2) 6-9.9 m, (3) 10-13.9, (4) 14-17.9 m, (5) 18-21.9 m, (6) 22-25.9 m, (7) 26-29.9 m, (8) ≥30 m.

Table 3.1. Species-specific parameter estimates of non-linear height-diameter at breast-height models using the Chapman-Richards function ($H = 1.3 + a(1 - e^{-b\,DBH})^{c}$) where H is tree height (m), DBH is tree diameter at breast-height (cm), a is an asymptote parameter, b is a scale parameter, c is a shape parameter.

	Parameter				
Species	a	b	c	$MS_{(error)}$	R^2
Balsam fir	28.807	0.036	1.021	5.484	0.577
Paper birch	21.770	0.071	0.896	6.332	0.412
Jack pine	20.301	0.149	3.161	7.486	0.610
Trembling aspen	25.909	0.127	2.706	12.238	0.626
Black spruce	25.659	0.047	1.138	3.807	0.687
White spruce	20.461	0.114	2.669	5.103	0.743

Calculations

Volume, BA, and Density

Individual tree and snag volumes were estimated using DBH and height measurements and Honer's (1983) volume equations which are species-specific (eq. 2):

$$[2] \qquad V = \frac{0.0043891 \times (DBH)^2 \times (1 - 0.04365 \times b_2)^2}{c_1 + 0.3048 \times \frac{c_2}{H}}$$

where V is tree or snag volume (m^3), DBH is diameter at breast-height (cm), H is tree or snag height (m), and b_2, c_1, c_2 are species-specific parameters published in Honer *et al.* (1983). Individual tree and snag volumes were summed to the plot level and then scaled to per hectare.

Basal area (m^2) of individual trees and snags by diameter class, height, and species were calculated using the following formula (eq. 3):

$$[3] \qquad BA = \pi(DBH/2)^2$$

where BA is the basal area (m^2) of an individual tree or snag and DBH (m) is the diameter of the tree or snag at breast-height. Individual BAs values were summed to plot level and then scaled to per hectare. Densities of trees and snags (stems/ha) were obtained by counts per plot and scaled to per hectare.

Structural Diversity

Quantification of tree- and snag-size diversity as a measure of stand structural diversity was performed using two indices on both DBH and height data: (a) Shannon's index (Shannon and Weaver 1949; Buongiorno *et al.* 1994; Staudhammer and Lemay 2001; Varga *et al.* 2005) (eq. 4) and (b) coefficient of variation (Staudhammer and Lemay 2001; Varga *et al.* 2005) (eq. 5).

$$[4] \qquad H' = -\Sigma[p_i \ln(p_i)]$$

where H' is Shannon's index and p_i is the proportion of BA of individuals in the ith DBH or height class compared with total stand BA.

[5] $$CV = \frac{s}{\bar{x}} \times 100$$

where CV is coefficient of variation, $\bar{x}$ is mean DBH or height, and s is standard deviation. Basal area was chosen for analysis in Shannon's index as it has been found to provide a more accurate assessment of tree-size diversity than density (Solomon and Gove 1999), possibly because it more accurately represents the occupation of trees on a site (Staudhammer and Lemay 2001). I constructed bar plots to show the density (stems/ha) of trees and snags by DBH and height classes for each TSF class (72-90, 139, and 201 year-old stands) and stand type.

Statistical Analysis

To determine if stand volume, BA, density, and structural diversity differed with TSF (continuous variable) and stand type (categorical variable), multiple regression analyses were conducted using the following model (Neter *et al.* 1996) (eq. 6):

[6] $$I' = b_o + b_1 A + b_2 A^2 + b_3 T + b_4 AT + b_5 A^2 T$$

where I' is predicted volume, BA, density, Shannon's index, or CV, b_i are coefficients, A is TSF in years and T is stand type. Insignificant A^2 and A^2T variables were removed from eq. 6 utilizing a backward stepwise procedure. Normality and homogeneous variances were confirmed following Neter *et al.* (1996). Statistical significance was based on $\alpha = 0.10$ and all statistical analysis was performed using SYSTAT® 10 2000 (SPSS Inc. 2000).

RESULTS

Volume, BA, and Density

Stand volume and BA of trees differed with TSF and stand type (Table 3.2, Figure 3.1A,B). In conifer stands, tree volume was lowest in 139 year-old stands and higher in 72-90

Table 3.2. Effects of time since fire (A) (years) and stand type (T) (C = conifer, M = mixedwood, and B = broadleaf) on stand volume (m^3/ha), basal area (BA) (m^2/ha), and density (stems/ha) of trees.

Characteristic	Source	df	MS	F	P
Volume	A	1	2.3	0.001	0.977
	A^2	1	101.2	0.035	0.852
	T	2	10,416.3	3.645	0.041
	A x T	2	16,413.4	5.744	0.009
	A^2 x T	2	18,211.3	6.373	0.006
	Error	24	2,857.5		
BA	A	1	17.5	0.691	0.414
	A^2	1	15.3	0.606	0.444
	T	2	140.1	5.569	0.010
	A x T	2	171.8	6.830	0.004
	A^2 x T	2	176.0	6.994	0.004
	Error	24	25.2		
Density	A	1	325,063	3.061	0.093
	A^2	1	316,864	2.984	0.097
	T	2	20,103	0.189	0.829
	A x T	2	14,429	0.136	0.874
	A^2 x T	2	9,549	0.090	0.914
	Error	24	106,196		

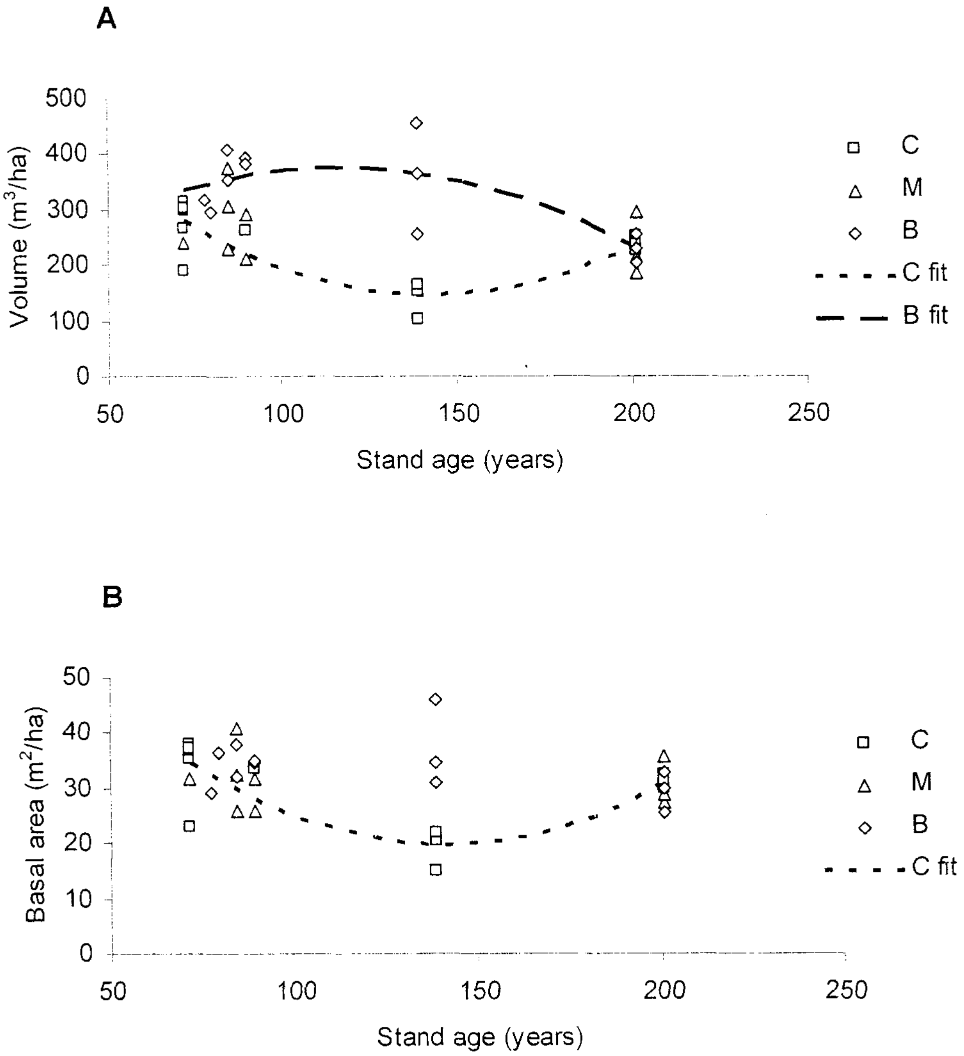

Figure 3.1. Relationships between (A) stand volume of trees (m^3/ha) and time since fire (TSF) (years) and type (when stand type = C, $Volume = 691.05168 - 7.63443A + 0.02673A^2$; when stand type = B, $Volume = 95.71548 + 4.82607A - 0.02073A^2$; when stand type = M, no significant relationship between volume and TSF found), (B) stand basal area of trees (BA) (m^2/ha) and TSF (years) and stand type (when stand type = C, $BA = 81.73090 - 0.87605A + 0.00310A^2$; when stand type = B or M, no significant relationship between BA and TSF was found), and (C) tree density (stems/ha) and TSF (years) ($Density = 31117.18434 - 35.08039A + 0.12216A^2$) where no significant relationship between density and stand type was found. Symbols represent C = conifer, M = mixedwood, and B = broadleaf.

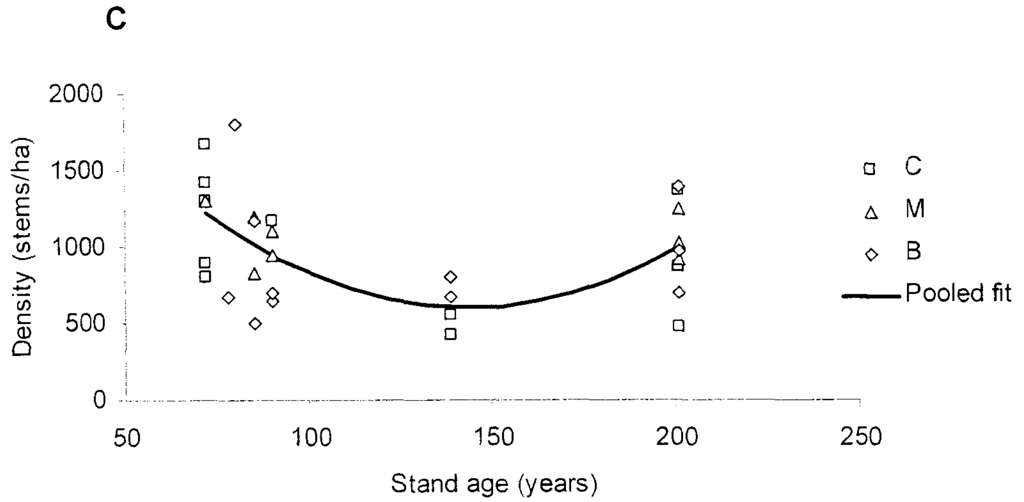

Figure 3.1. (Continued).

and 201 year-old stands ($R^2 = 0.70$, $P = 0.005$) (Figure 3.1A). Broadleaf stands showed a contrasting trend, being highest in 139 year-old stands and lower in 72-90 and 201 year-old stands ($R^2 = 0.57$, $P = 0.022$) while tree volume in mixedwood stands did not differ with TSF in stands 72 to 201 years of age (Figure 3.1A). Tree BA in conifer stands responded similarly to TSF as conifer tree volume ($R^2 = 0.65$, $P = 0.009$) while tree BA in broadleaf and mixedwood stands did not change with TSF (Figure 3.1B). Further, all three stand types had similar tree volumes and BAs in 72-90 and 201 year-old stands respectively while 139 year-old broadleaf stands had a higher tree volume and BA than 139 year-old conifer stands (Figure 3.1A,B). Tree density differed with TSF but not stand type (Table 3.2, Figure 3.1C). The lowest density was in 139 year-old stands, followed by 201 and 72-90 year-old stands ($R^2 = 0.32$, $P = 0.003$) (Figure 3.1C).

Snag volume did not significantly differ with TSF nor stand type, but snag BA was affected by TSF and stand type (Table 3.3, Figure 3.2A,B). In conifer stands, snag BA increased linearly with TSF ($R^2 = 0.36$, $P = 0.041$), but no significant relationship was found between snag BA and TSF for other stand types (Figure 3.2B). Snag BA did not vary significantly among stand types for stands aged between 72-139 years, but conifer stands had a significantly higher snag BA than other stand types in 201 year-old stands (Figure 3.2B). Snag density did not differ with TSF nor stand type (Table 3.3, Figure 3.2C).

Table 3.3. Effects of time since fire (A) (years) and stand type (T) (C = conifer, M = mixedwood, and B = broadleaf) on stand volume (m^3/ha), basal area (BA) (m^2/ha), and density (stems/ha) of snags.

Characteristic	Source	df	MS	F	P
Volume	A	1	191. 3	0.269	0.608
	T	2	207. 5	0.292	0.749
	A x T	2	938.8	1.319	0.284
	Error	27	711.7		
BA	A	1	50.6	3.239	0.083
	T	2	15.3	0.982	0.388
	A x T	2	43.9	2.814	0.078
	Error	27	15.6		
Density	A	1	12,900	0.323	0.575
	T	2	34,486	0.863	0.433
	A x T	2	29,152	0.729	0.492
	Error	27	39,978		

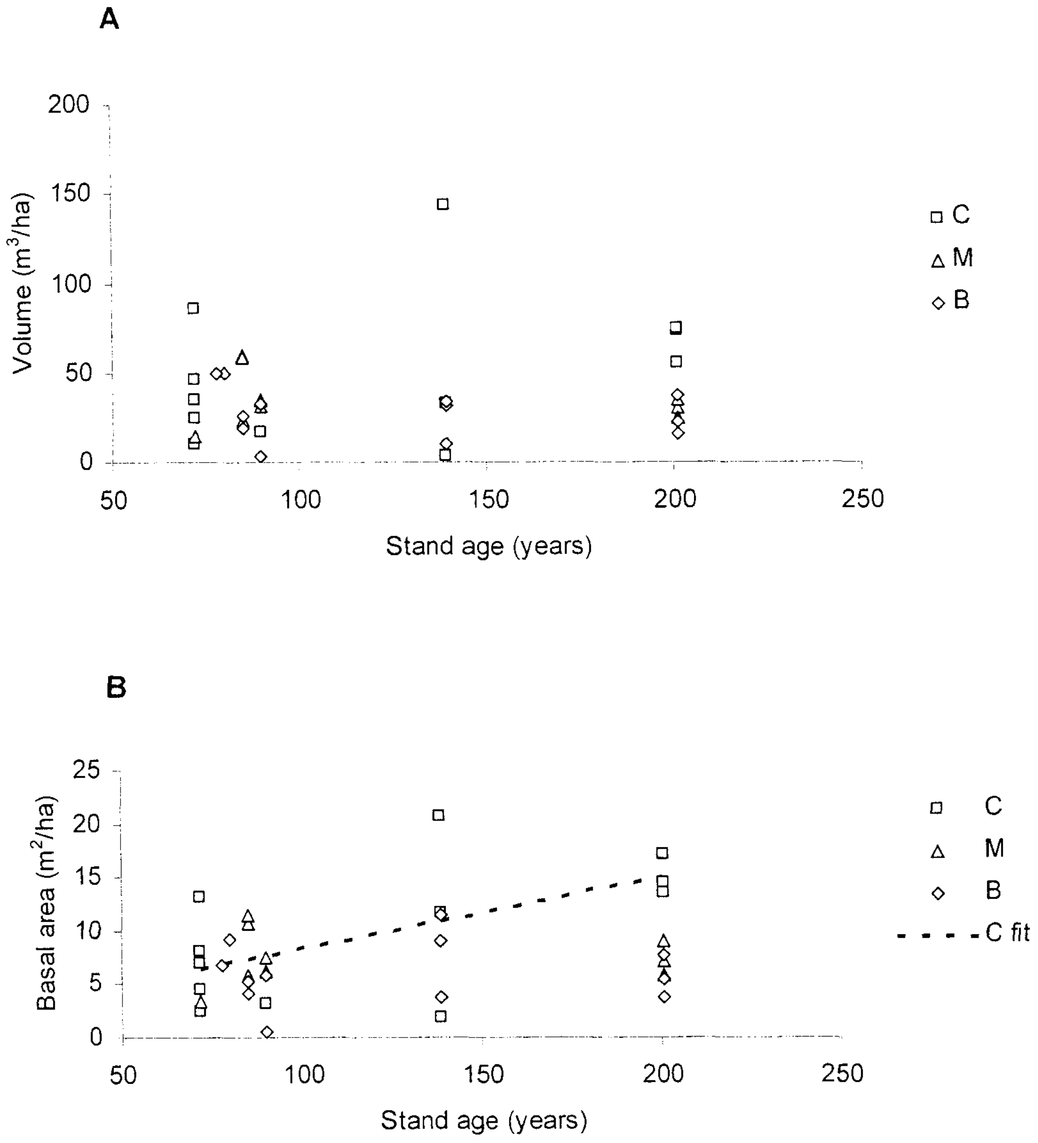

Figure 3.2. Relationships between (A) snag volume (m^3/ha) and time since fire (TSF) (years) and stand type (no significant relationship was found), (B) snag basal area (BA) (m^2/ha) and TSF (years) and stand type (when stand type = C, $BA = 1.55582 + 0.06742A$; when stand type = B or M, no significant relationship between BA and TSF was found), and (C) snag density (stems/ha) and TSF (years) and stand type (no significant relationship was found). Symbols represent C = conifer, M = mixedwood, and B = broadleaf.

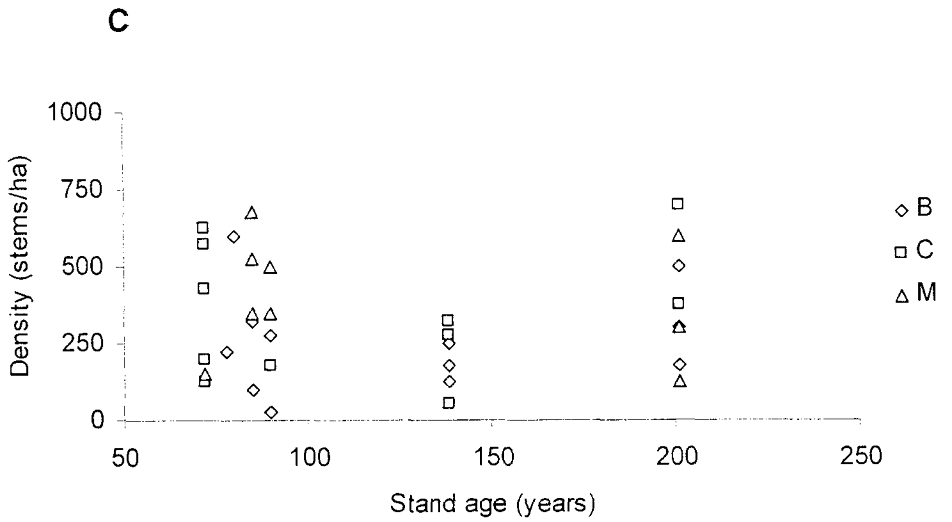

Figure 3.2. (Continued).

Structural Diversity

Structural diversity, measured using DBH-based Shannon's index, did not change with TSF, but differed significantly with stand type (Table 3.4, Figure 3.3A). Mixedwoods had highest DBH-based Shannon's index, followed by conifer and broadleaf stands (Figure 3.3A). Height-based Shannon's index differed with TSF and stand type (Table 3.4, Figure 3.3B). For broadleaf stands, height-based Shannon's index peaked in 139 year-old stands and was lower in 72-90 and 201 year-old stands ($R^2 = 0.62$, $P = 0.012$) (Figure 3.3B). In conifer and mixedwood stands, height-based Shannon's index was unaffected by TSF (Figure 3.3B). Height-based Shannon's index was similar for all three stand types in 72-90 and 201 year-old stands respectively while 139 year-old broadleaf stands had a higher height-based Shannon's index than conifer stands (Figure 3.3B).

Table 3.4. Effects of time since fire (A) (years) and stand type (T) (C = conifer, M = mixedwood, and B = broadleaf) on Shannon's index (*H'*) and coefficient of variation (CV).

Index	Source	df	MS	F	P
H'					
DBH-based	A	1	0.004	0.204	0.655
	T	2	0.083	4.745	0.017
	A x T	2	0.033	1.898	0.169
	Error	27	0.017		
Height-based	A	1	0.087	5.278	0.031
	A^2	1	0.090	5.445	0.028
	T	2	0.040	2.399	0.112
	A x T	2	0.048	2.892	0.075
	A^2 x T	2	0.046	2.752	0.084
	Error	24	0.017		
CV					
DBH-based	A	1	17.1	0.474	0.498
	A^2	1	13.0	0.361	0.553
	T	2	255.7	7.089	0.004
	A x T	2	233.7	6.479	0.006
	A^2 x T	2	224.3	6.218	0.007
	Error	24	36.1		
Height-based	A	1	386.2	8.356	0.008
	A^2	1	380.7	8.237	0.008
	T	2	9.8	0.213	0.810
	A x T	2	14.8	0.321	0.728
	A^2 x T	2	18.6	0.403	0.673
	Error	24	46.2		

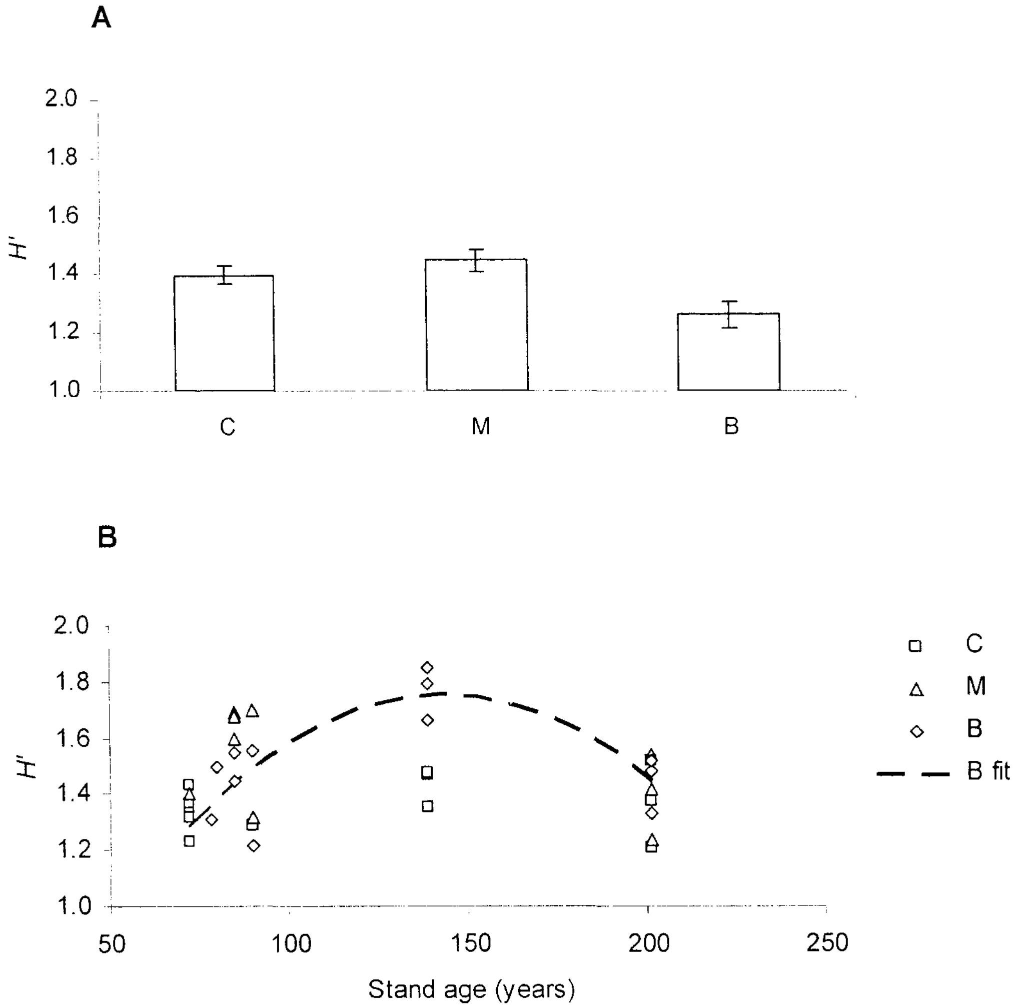

Figure 3.3. Relationships between (A) DBH-based Shannon's index (*H'*) and stand type (no significant relationship between *H'* and time since fire (TSF) was found) and (B) height-based Shannon's index (*H'*) and TSF (years) and stand type (when stand type = B, $H' = -0.15262 + 0.02659A - 0.00009A^2$; when stand type = C or M, no significant relationship between *H'* and TSF was found). Symbols represent C = conifer, M = mixedwood, and B = broadleaf. Error bars represent +1 standard error of the mean.

Diameter at breast-height-based CV also differed significantly with TSF and stand type (Table 3.4, Figure 3.4A). In broadleaf stands, it followed an inverse U-shaped distribution with TSF where diversity was highest in 139 year-old stands and lower in 72-90 and 201 year-old stands ($R^2 = 0.70$, $P = 0.004$), whereas in conifer and mixedwood stands, DBH-based CV was unaffected by TSF (Figure 3.4A). DBH-based CV did not differ with stand type in 72-90 and 201 year-old stands respectively while 139 year-old broadleaf stands had a higher DBH-based CV than conifer stands (Figure 3.4A). Height-based CV also differed with TSF while having no stand type effect (Table 3.4, Figure 3.4B). Using this index, 139 year-old stands were found to be the most diverse with 72-90 and 201 year-old stands being lower ($R^2 = 0.41$, $P < 0.001$) (Figure 3.4B).

Tree and snag density was highest in the smallest DBH class and decreased as DBH class increased in 72-90 (Figure 3.5A,D,F) and 201 (Figure 3.5C,E,H) year-old stands, with the exception that class 5 had slightly higher tree and snag density than class 4 in 201 year-old conifer stands (Figure 3.5C). In 139 year-old stands, trees and snags were distributed more evenly among the DBH classes with classes 1 and 3 having the highest tree and snag density in conifer stands while classes 1 and 5 had the highest density of trees and snags in broadleaf stands (Figure 3.5B,G). Further, these peaks also caused the distribution of trees and snags among the DBH classes in 139 year-old stands to be weakly bimodal.

Trees and snags were more normally distributed among the height classes in 72-90 year-old conifer and mixedwood stands (Figure 3.6A,D) and 201 year-old mixedwood and broadleaf stands (Figure 3.6E,H). A bimodal distribution of trees and snags among the height classes occurred in 139 year-old conifer (Figure 3.6C) and broadleaf (Figure 3.6G) stands, with peaks in classes 2 and 4 and 3 and 7, respectively. A weak bimodal distribution of trees and snags among the height classes also occurred in 139 year-old conifer stands (Figure 3.6B) and 72-90 year-old broadleaf stands (Figure 3.6F).

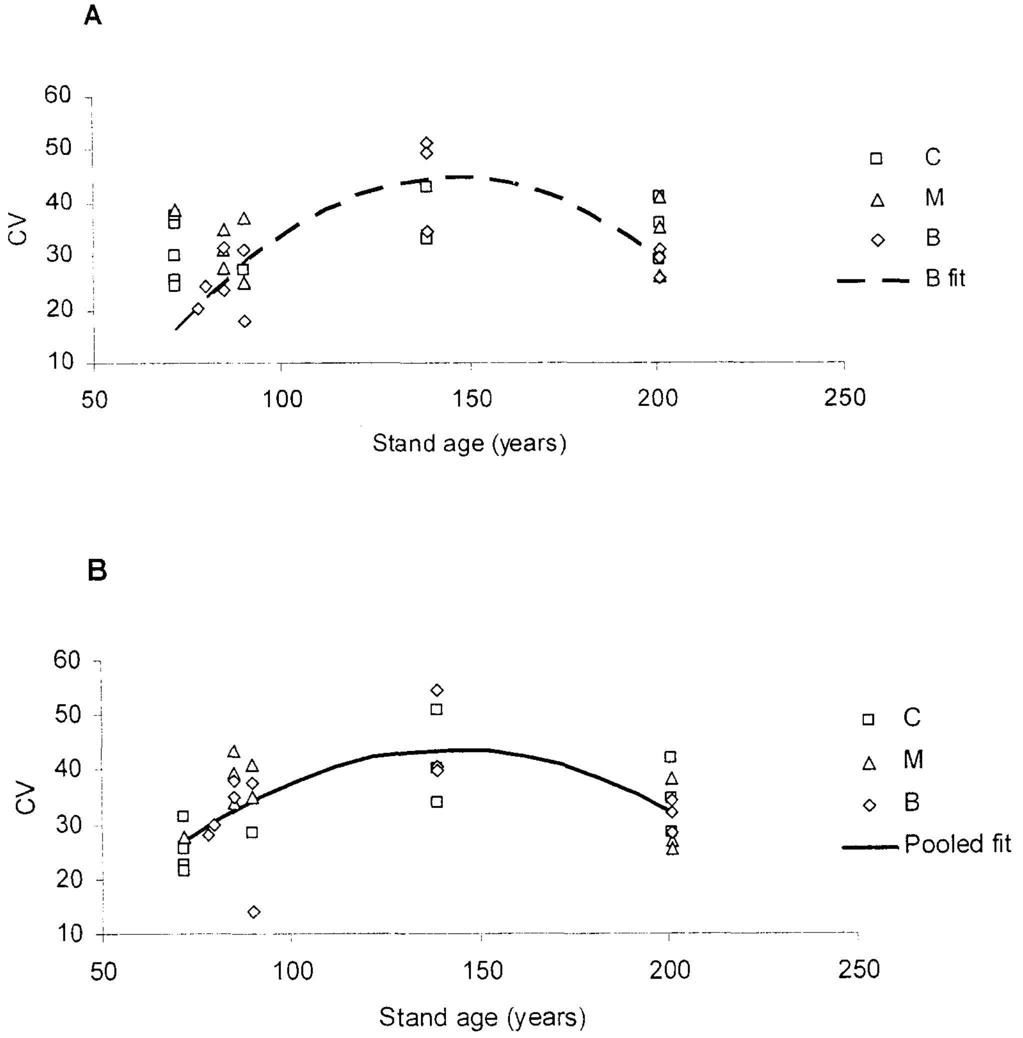

Figure 3.4. Relationship between (A) DBH-based coefficient of variation (CV) and time since fire (TSF) (years) and stand type (when stand type = B, $CV = -66.59319 + 1.52583A - 0.00522A^2$; when stand type = C or M, no significant relationship between CV and TSF was found) and (B) height-based coefficient of variation (CV) and TSF (years) ($CV = -24.60307 + 0.95764A - 0.00336A^2$) where no significant relationship between CV and stand type was found. Symbols represent C = conifer, M = mixedwood, and B = broadleaf.

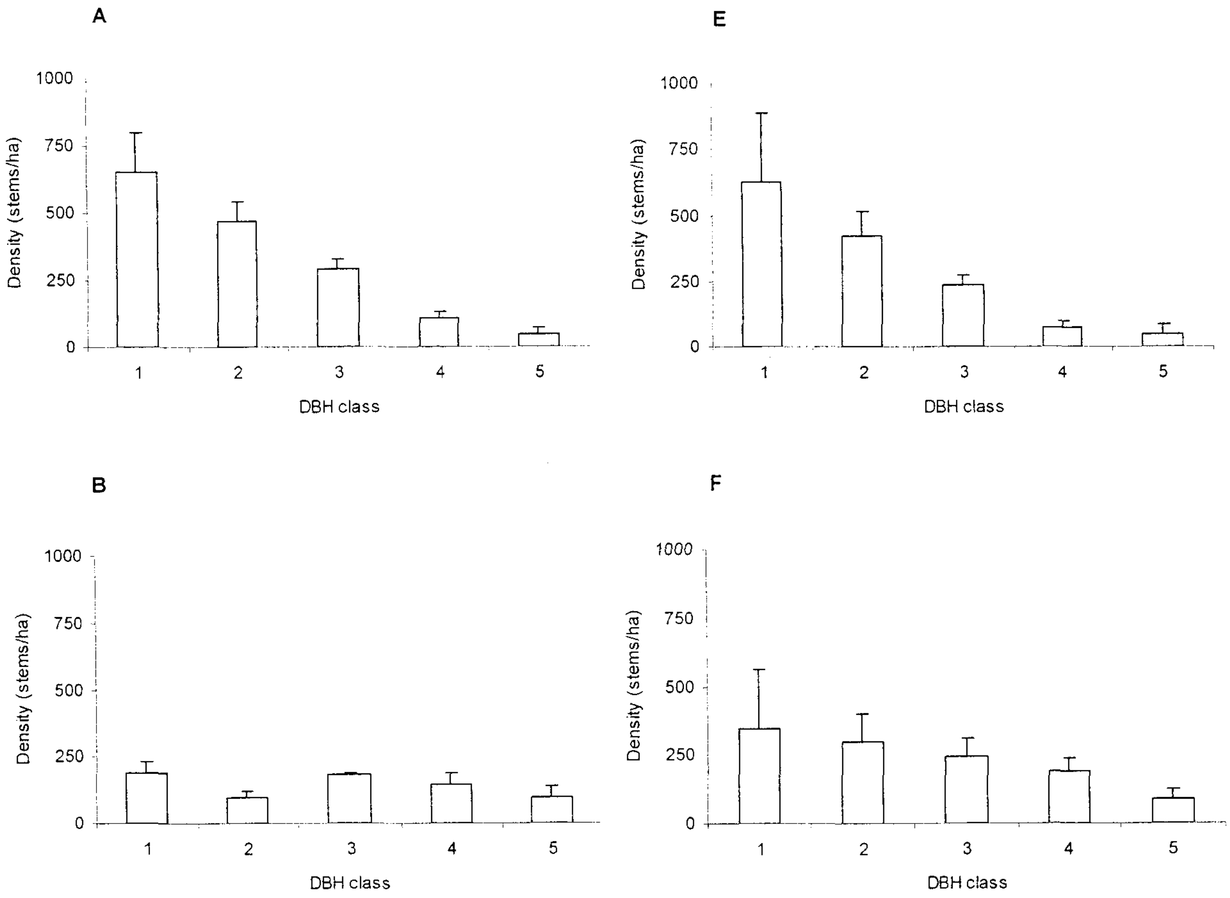

Figure 3.5. Density of trees and snags (stems/ha) by diameter at breast-height (DBH) class (1 = 10-14.9 cm, 2 = 15-19.9 cm, 3 = 20-24.5 cm, 4 = 25-29.9 cm, and 5 ≥ 30 cm) for (A) 72-90 year-old conifer, (B) 139 year-old conifer, (C) 201 year-old conifer, (D) 72-90 year-old mixedwood, (E) 201 year-old mixedwood, (F) 72-90 year-old broadleaf, (G) 139 year-old broadleaf, and (H) 201 year-old broadleaf stands. Error bars represent +1 standard error of the mean.

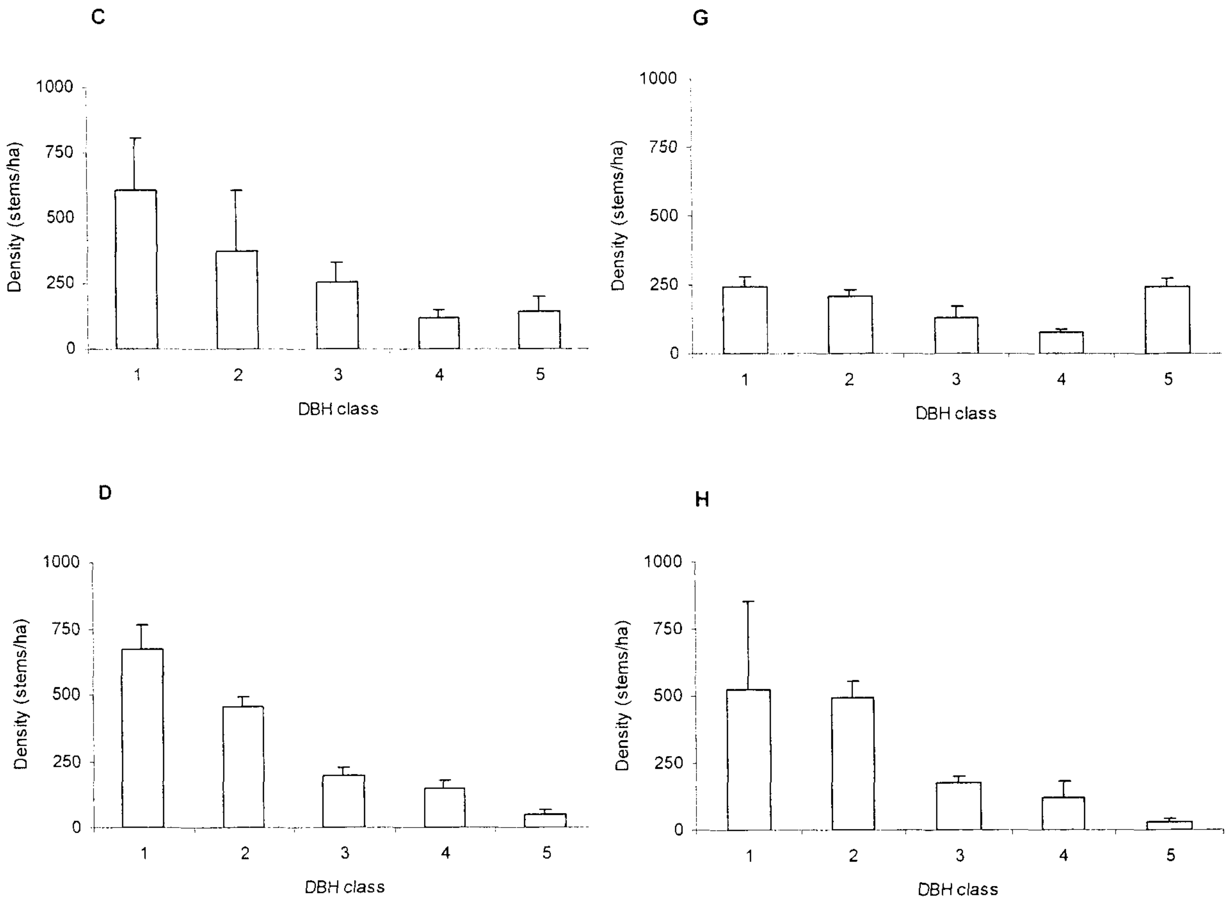

Figure 3.5. (Continued).

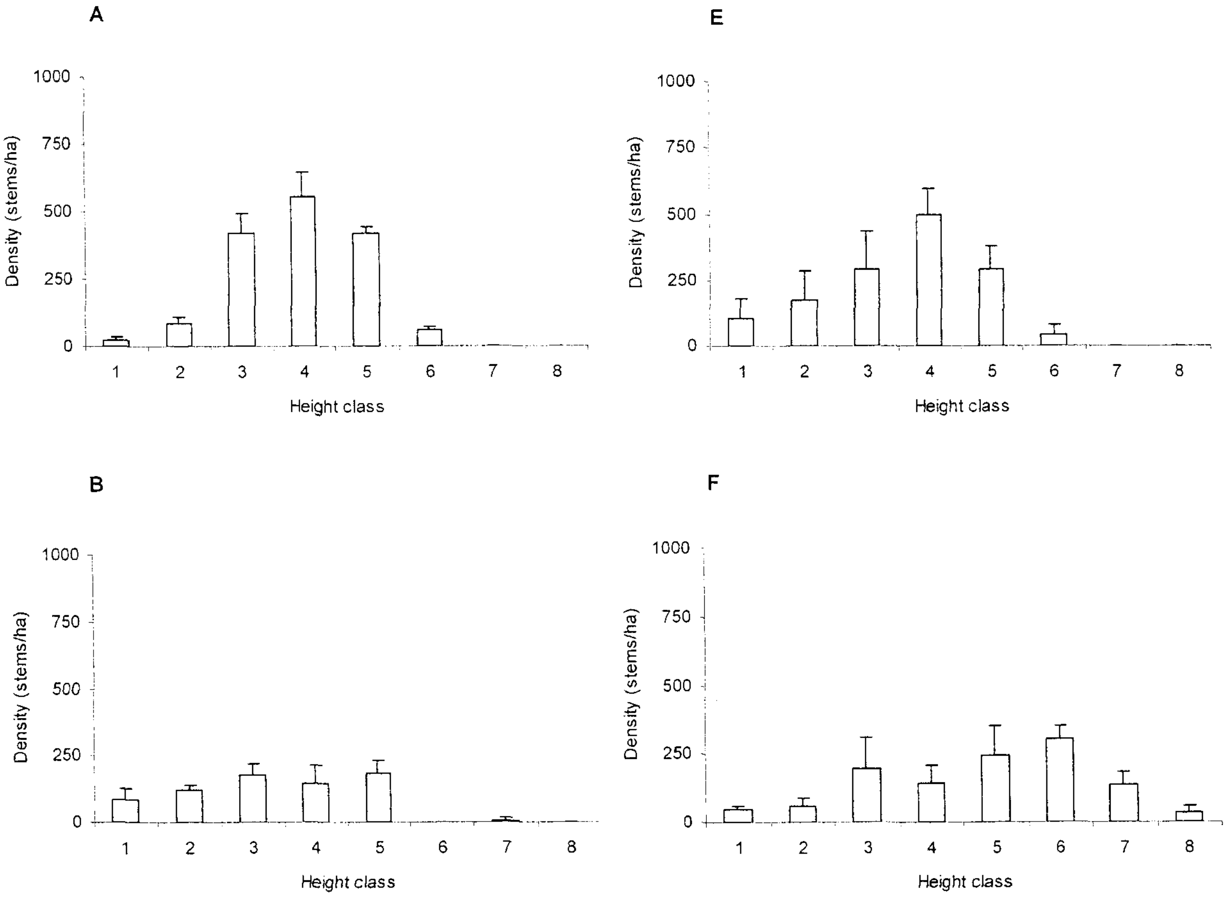

Figure 3.6. Density of trees and snags (stems/ha) by height class (1 = 2-5.9 m, 2 = 6-9.9 m, 3 = 10-13.9 m, 4 = 14-17.9 m, 5 = 18-21.9 m, 6 = 22-25.9 m, 7 = 26-29.9 m, and 8 ≥ 30 m) for (A) 72-90 year-old conifer, (B) 139 year-old conifer, (C) 201 year-old conifer, (D) 72-90 year-old mixedwood, (E) 201 year-old mixedwood, (F) 72-90 year-old broadleaf, (G) 139 year-old broadleaf, and (H) 201 year-old broadleaf stands. Error bars represent +1 standard error of the mean.

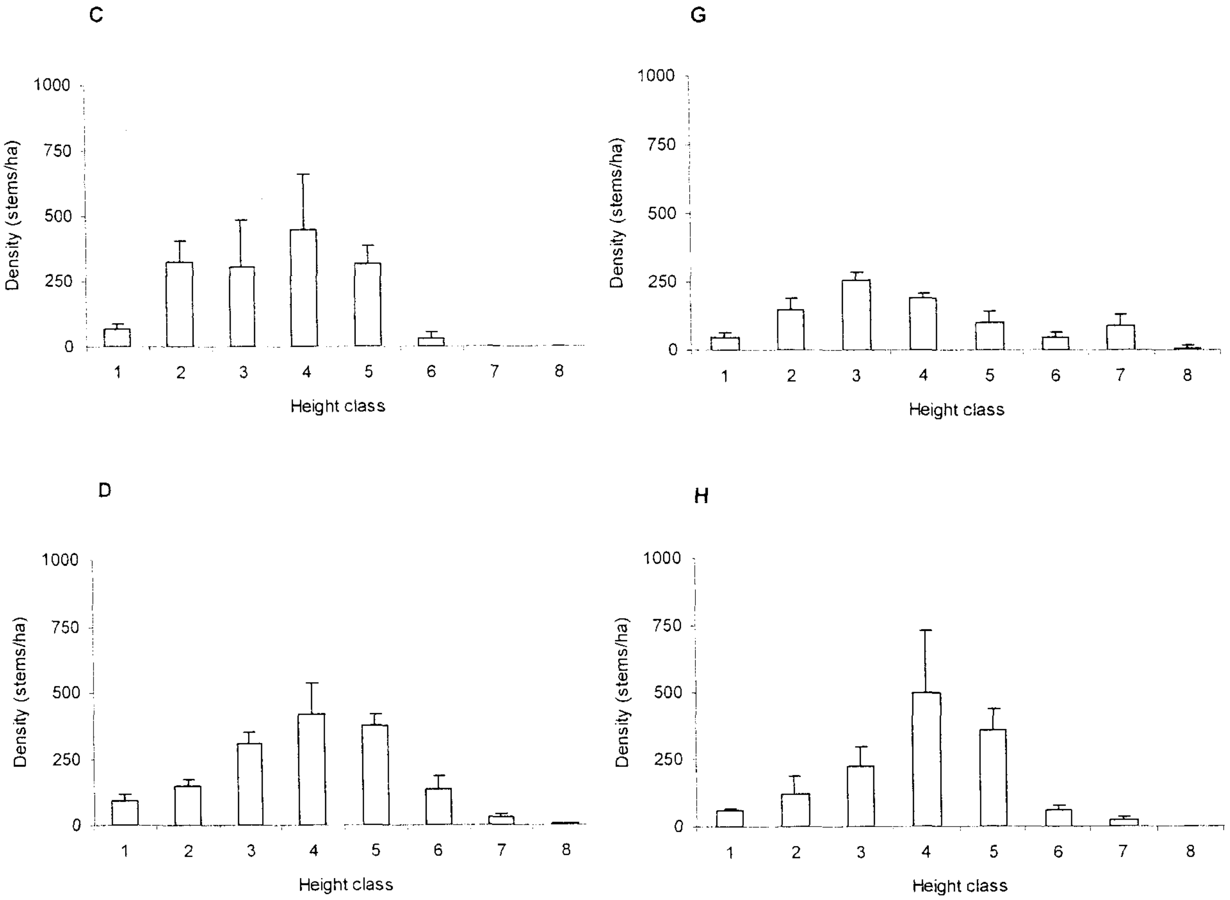

Figure 3.6. (Continued).

DISCUSSION

Relationships between TSF and Stand Type, and Volume, BA, and Density

Tree volume in broadleaf stands followed an inverse U-shaped pattern, whereas tree volume and BA in conifer stands followed a U-shaped pattern. In broadleaf stands, the higher stand volume in stands of age 139 years compared to those of 72-90 years is attributed to the growth in biomass of the stand as the trembling aspen trees grow larger. However, as the stand develops beyond 139 years of age, the resulting decline in stand volume is the consequence of the disappearance of the pioneering trembling aspen cohort. In conifer stands, the lower volume in stands of 139 years of age is attributed to the disappearance of pioneering jack pine. While trembling aspen is considered to be a shorter-lived tree species than jack pine (Burns and Honkala 1990; Farrar 1995), only one or two living jack pine trees remained from the pioneering cohort per 400 m^2 plot in 139 year-old conifer stands (average number of pioneering jack pine trees per hectare = 42) while several trembling aspen trees (6-11 per 400 m^2 plot) from the pioneering cohort were still living in 139 year-old broadleaf stands (average number of pioneering trembling aspen trees per hectare = 200). I believe that the ability of trembling aspen to persist to such an old age is related to site quality, as trembling aspen can attain ages and sizes well beyond their average on productive sites (Farrar 1995). The greater longevity of trembling aspen than jack pine was further evidenced by amount of coarse wood debris on my study sites.

Similar to my finding that stand volume of trees decreased with TSF after maturation, Paré and Bergeron (1995) reported that above-ground tree biomass in trembling-aspen-dominated forests decreased linearly from stand ages of 75 to 197. Further, Delong and Kessler (2000) reported that 41-140 year-old stands had higher stand volumes of trees than 140+ years-old stands in conifer forests in the sub-boreal forests of British Columbia, Canada.

The U-shaped pattern in tree density that I found to occur from 72 to 201 years TSF for all stand types is supported by Lee *et al.* (1997), who reported that tree density in 51-63 year-old stands was 1247 stems/ha and decreased in 97-311 year-old stands to 535 stems/ha in trembling-aspen-dominated forests. As a stand ages from 72 to 139 years of age, the trees in the stand are growing larger and require more growing space and nutrients in the process (Oliver and Larson 1996; Chen and Popadiouk 2002). As such, the stand can not support as many individuals and tree density declines. However, beyond 139 years of age, the large pioneering trees die off and free up growing space and resources, allowing many smaller individuals to occupy the site at canopy and subcanopy positions.

Tree death, either from competition, disease and insects, or longevity-related mortality, results in an input of snags (Greif and Archibold 2000). Clark *et al.* (1998) found similar snag BA trends in conifer stands as I did, reporting that snag BA and density increases from a stand age of 51 years to a stand age of 250 years in conifer-dominated forests in sub-boreal British Columbia, Canada. For stands of 72-90 year-old, intense self-thinning has long since come to an end while the stand would still be too young to experience significant longevity-related tree death, causing snag BA to be quite low. As the stands become 139 years of age, most of the pioneering trees in conifer stands have died off and stand BA increases due to the contribution of these trees to snag BA values. In 201 year-old stands, gap dynamic processes would have caused an input of a large number of smaller snags, resulting in higher snag volumes.

Relationships between TSF and Stand Type and Structural Diversity

Diversity indices are becoming increasing popular in forest ecology as a means of quantitatively evaluating diversity (Lähde *et al.* 1999). Although there are many indices that can be used to evaluate structural diversity, Shannon's index and CV are two of the most popular (Shannon and Weaver 1949; Buongiorno *et al.* 1994; Staudhammer and Lemay 2001; Varga *et al.* 2005). Three of the four diversity indices (height-based Shannon's index, DBH-based CV, and height-based CV) showed that structural diversity varied with stand age while DBH- and height-based Shannon's indices and DBH-based CV varied with stand type.

Shannon's index is maximized when trees are reversely-J distributed among the size classes when the proportions are calculated based on basal area (Buongiorno *et al.* 1994; Staudhammer and Lemay 2001; Varga *et al.* 2005). DBH-based Shannon's index was not affected by TSF, but differed significantly among stand types. Height-based Shannon's index followed an inverse U-shaped pattern with stand age in broadleaf stands, but did not differ in other stand types. The different responses of height-based Shannon's index to stand age among stand types may be attributed to the proportion of pioneering species in relation to later successional species. In 72-90 year-old stands of all three stand types, the majority of the trees are from the pioneering cohort and are relatively homogeneous in tree height. During this period of development, the component of later successional species that are at tree-size (defined as DBH ≥10 cm in this study) is low. As such, structural diversity (measured using height-based Shannon's index) is relatively low due to the largely homogeneous heights of pioneering trees in the stand and the small component of later successional trees causing most of the trees in the stand to be distributed among a narrow range of height classes.

Once the stand becomes 139 years of age, there is a difference in structural diversity between conifer and broadleaf stands as measured by height-based Shannon's index. In broadleaf stands, stands were composed of several tall trembling aspen trees and some shorter late successional trees that established at various times throughout succession. In conifer stands of this age, most jack pine trees have died off, resulting in less representation of trees in larger height classes. This leads to lower structural diversity compared to broadleaf stands and no significant difference in structural diversity from that in 72-90 year-old conifer stands occurs due to a less significant contribution from the pioneering cohort.

Zenner (2004) suggested that old-growth forests (equivalent to my 201 year-old stands) may be no more structurally complex than mature forests. In the 201 year-old stands, I found that structural diversity once again was lower in all three stand types, as the pioneering cohort had completely died off and the stand was composed of almost exclusively late successional tree species. The lower diversity in the oldest stands in my study was largely attributed to the disappearance of the pioneering cohorts that are typically larger in size than their successors (Burns and Honkala 1990; Farrar 1995).

Because height-based Shannon's index showed a stand-age effect while DBH-based Shannon's index did not suggests that height-based Shannon's index may be able to detect finer, more subtle changes in structural diversity than DBH-based Shannon's index. However, I make this statement with caution, as differences between the two measure's relative abilities to detect variations in structural diversity may be due to the use of narrower class widths in height-based analysis (4-cm width) compared to DBH-based analysis (5-cm width). The creation of arbitrary size classes as a weakness of Shannon's index has also been identified by Edgar and Burk (2001) and Varga *et al.* (2005).

Coefficient of variation is maximized when a two-storied stand structure is produced (bimodal) (Buongiorno *et al.* 1994; Staudhammer and Lemay 2001; Varga *et al.* 2005). DBH-based CV showed that broadleaf stands followed an inverse U-shaped pattern with stand age, while conifer and mixedwood stands were not affected by stand age. Height-based CV followed an inverse U-shaped pattern with stand age regardless of stand type. Similar to Shannon's index, CV was low in 72-90 year-old stands for all three stand types as the trees were distributed within a narrow range of diameters and heights, attributed again to the largely homogeneous DBHs and heights of pioneering trees and the small component of later successional trees [illegible] the stands.

Measured using DBH-based CV, once a stand became 139 years of age, broadleaf stands were more structurally diverse than 72-90 year-old stands, attributed to several large pioneering trembling aspen trees and smaller late successional trees creating a bimodal stand structure. In conifer stands of this age, most of the jack pine trees have died off resulting in a less pronounced bimodal structure and a lower structural diversity compared to broadleaf stands as 139 year-old conifer stands are no more structurally diverse statistically than 72-90 year-old stands statistically. However, using height-based CV, both 139 year-old broadleaf and conifer stands showed an increase in structural diversity from 72-90 year-old stands, suggesting that height-based CV may be able to detect stand modality more than DBH-based CV. Alternatively, the difference between DBH- and height-based CV could be attributed to the taper effects of species, size, and their growing environment. Measured by both CV indices, the lower structural diversity in the 201 year-old stands for all three stand types is attributed to the pioneering cohort completely dying off and the stand becoming composed of almost exclusively late successional tree species that do not differ greatly in DBH and height.

My findings are supported by Varga *et al.* (2005) who found tree-canopy differentiation from a bimodal to a multi-modal structure as stands age in shade tolerant western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* (Donn ex D. Don) Spach) forests in western Canada. Further, Paré and Bergeron (1995) reported similar structural trends, finding that the vertical distribution of cumulative crown width develops from a single layer at the age of 27 years, to being bimodal at the age between 47 to 121 years, to multi-modal at the age of 144 to 168 years, and to a continuous layer at an age of 231 years. While I was unable to find mixedwood stands of 139 years of age in my study area to sample, I believe that mixedwood stands of this age in this study region, similar to the stand of 121 year-old mixedwoods in Paré and Bergeron's (1995) study, would be more diverse than their single-species counterparts because mixedwoods composed of tree species with different resource requirements and growth and structural characteristics would promote a more heterogeneous canopy (Edgar and Burk 2001; Varga *et al.* 2005).

Forest Management Implications for the Maintenance and Creation of Structural Diversity

Many studies have focused on managing forests for structural attributes such as large trees and snags, certain species compositions, desired volumes, BAs, or densities of live trees or snags. However, as structural diversity is a relatively new concept in forest ecology, this section will focus on options for managing forests for structural diversity as it affects wildlife habitat and maintaining biodiversity (MacArthur and MacArthur 1961; Willson 1974; Ambuel and Temple 1983; Buongiorno *et al.* 1994; Kimmins 1997; Lõhmus and Lõhmus 2001). For example, MacArthur and MacArthur (1961) and Willson (1974) discovered that bird-species diversity increased with increases in foliage height diversity and stand composition. Further, Payer and Harrison (2003) found that American marten (*Martes americana* Turton) preferred forests that contained tall trees, high tree BA, a healthy broadleaf component, and high snag volumes. As well, voles (*Clethrionomys* spp.) (Ecke *et al.* 2002) and deer mice (*Peromyscus maniculatus* Wagner) (Pearce and Venier 2005) prefer mature, closed and tall forest canopies that are heterogeneous in structure. Because of this, it has been suggested that forest management activities that strive for tree-size diversity can be used to enhance wildlife habitat and maintain biodiversity (Buongiorno *et al.* 1994).

Forest management has traditionally been regarded as having a negative impact on forest biodiversity and wildlife habitat by reducing tree-size diversity (Swindel *et al.* 1991; McRae *et al.* 2001). Traditional clearcut logging generally lowers tree-size diversity by removing most of the trees on a site and leaving only a few trees, the characteristics and quantities of which depend on government standards and practices (Wikström and Eriksson 2000; Ontario Ministry of Natural Resources 2001). Further, partial harvesting can result in lower tree-size diversity, as harvested trees are largely the most economically viable trees, which provide a large proportion of the vertical structural heterogeneity that occurs in a stand (Buongiorno *et al.* 1994).

Management options are available to increase tree-size diversity at both the stand and landscape level through forest management practices. One option would be to lengthen the rotation cycle, allowing more stands to reach overmature (equivalent to my 139 year-old stands) and old-growth (equivalent to my 201 year-old stands) stages of development (Buongiorno *et al.* 1994). This could help to create a wide range of stand ages on the managed landscape (similar to what is done naturally by fire), thereby increasing tree-size diversity at the landscape level. In contrast, partial harvesting could be used in mature (equivalent to my 72-90 year-old stands), even-aged, homogeneous diameter and height stands to increase tree-size diversity (at the stand level) in the future stand by maintaining some older, large pioneering trees, releasing suppressed understory trees and saplings, and allowing seedlings to establish by freeing up growing space and increasing available light and nutrients (Wikström and Eriksson 2000; Sullivan *et al.* 2001). However, managing for tree-size diversity may result in economic losses, which may not be desirable from a fibre-supply perspective (Buongiorno *et al.* 1994; Önal 1997; Wikström and Eriksson 2000). I recommend that forest management guidelines dedicated to providing wildlife habitat and maintaining biodiversity include consideration of tree-size diversity as a key stand structural element.

CHAPTER FOUR COARSE WOODY DEBRIS DYNAMICS OF BOREAL CONIFER, MIXEDWOOD, AND BROADLEAF FIRE- AND CLEARCUT LOGGING-ORIGIN STANDS IN CENTRAL CANADA

INTRODUCTION

Coarse woody debris (CWD) (defined as standing dead trees (snags) and downed woody debris (DWD) in this chapter) provides a variety of ecosystem services including maintaining wildlife habitat (Tallmon and Mills 1994; Robb *et al.* 1996; Imbeau *et al.* 1999; Bowman *et al.* 2000; Sedgeley 2001; Payer and Harrison 2003), storing water (Fraver *et al.* 2002) and carbon (Krankina and Harmon 1995; Fleming and Freedman 1998; Wang *et al.* 2002; Yatskov *et al.* 2003; Manies *et al.* 2005), increasing biodiversity (Kolström 1998; Lõhmus and Lõhmus 2001; Sippola *et al.* 2005), stabilizing nutrients after disturbance (Harmon and Hua 1991; Laiho and Prescott 2004), and facilitating forest regeneration (Hofgaard 1993; Takahashi 1994; Narukawa *et al.* 2003; Parent *et al.* 2003; Lampainen *et al.* 2004).

The accumulation pattern of CWD in the boreal forest follows a sigmoid distribution with time since stand-replacing fire (TSF), where large quantities of pre-disturbance CWD decline in a logarithmic fashion while an exponential increase in post-disturbance inputs occurs as a stand ages, with a decrease occurring in very old stands (Sturtevant *et al.* 1997; Clark *et al.* 1998; Delong and Kessler 2000; Hély *et al.* 2000a; Harper *et al.* 2005; Brassard and Chen 2006). Pre-disturbance CWD originates from trees killed during the fire and from CWD that is not consumed during the fire (Lee *et al.* 1997; Sturtevant *et al.* 1997; Spies *et al.* 1988). Both these inputs are usually high and contribute significantly to the structure of the stand following fire (Lee *et al.* 1997; Sturtevant *et al.* 1997; Harper *et al.* 2005). Post-disturbance inputs of CWD take time to develop, as they are driven by tree mortality caused by competition during self-thinning (Sturtevant *et al.* 1997; Chen and Popadiouk 2002), longevity (Lee *et al.* 1997; Hély *et al.* 2000a), and non-stand-replacing disturbances such as spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks (Blais 1981; Morin 1994; Fraver *et al.* 2002; Bouchard *et al.* 2005) and blowdown (Clark *et al.* 1998; Kulakowski and Veblen 2003).

Stand tree species composition may affect CWD characteristics (defined as types, volume, species, and decay) as it influences forest productivity and stand structure of live trees (MacPherson *et al.* 2001; Chen *et al.* 2003; Légaré *et al.* 2005; Varga *et al.* 2005; Brassard and Chen 2006). However, while studies have explored changes in CWD characteristics over time in various conifer (Clark *et al.* 1998; Linder 1998; Hély *et al.* 2000a; Harper *et al.* 2005) or trembling aspen (*Populus tremuloides* Michx.)-dominated (Lee *et al.* 1997; Lee 1998) fire-origin forest stands, no study has investigated CWD dynamics of mixedwood stands. Furthermore, effects of stand composition on CWD structural dynamics have not been examined under similar environmental conditions, such as soils, topography, and climate. By understanding the effect of stand composition on CWD dynamics, the impact of management activities that alter natural stand compositional trajectories on CWD dynamics can be determined.

Clearcut logging (referred to as clearcutting in this chapter) is applied in the boreal forest with the intent that to some extent, it emulates wildfires (Ontario Ministry of Natural Resources 2001). However, it is evident that the dynamics of many CWD characteristics (i.e., types, sizes, and amounts) are different in stands with clearcut- compared to fire-origin (Fleming and Freedman 1998; Linder and Östlund 1998; Sippola *et al.* 1998; McRae *et al.* 2001; Krankina *et al.* 2002; Pedlar *et al.* 2002; Rouvinen *et al.* 2002), which raises questions on the extent that clearcutting effectively emulates wildfires. While fire kills trees, scorches tree crowns, and burns roots systems, thereby creating new dead organic material, clearcutting disrupts the production and accumulation of CWD in a stand by removing organic material for commercial usage (Johnson 1992; Sippola *et al.* 1998; McRae *et al.* 2001).

The implications of clearcutting on CWD in comparison to fire as a stand-replacing disturbance mechanism have been explored in several European studies (e.g., Linder and Östlund 1998; Sippola *et al.* 1998; Krankina *et al.* 2002; Pedlar *et al.* 2002; Rouvinen *et al.* 2002) and in the Canadian boreal forest (e.g., Fleming and Freedman 1998; Pedlar *et al.* 2002; Martin *et al.* 2005), but most of the work has compared young clearcut-origin stands to old fire-origin stands. Therefore, a study that characterizes the CWD dynamics of fire-origin and clearcut stands with various stand compositions under similar environmental conditions and similar stand ages will help improve understanding of the consequences of clearcutting on forest stand structural dynamics and allow more ecologically sustainable management decisions to be made.

The goal of this study was to further understanding of the CWD stand structural dynamics as affected by stand composition, origin, and stand development in the central region of the boreal mixedwood forest in Canada. On glacial tills in this region, both single- and mixed-species stands of broadleaves and conifers are common (Rowe 1972). At early stages of stand development, jack pine (*Pinus banksiana* Lamb.) and trembling aspen are dominant species. At later stages of development, dominant conifers include black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* L.), while paper birch (*Betula papyrifera* Marsh.) is a dominant broadleaf species. Specific objectives were to: (1) characterize how CWD (snags and DWD) volume, basal area (BA) (snags only), density, species, and decay (DWD only), change with TSF, (2) quantify whether these structural attributes differ with stand composition, and (3) test to what extent fire and clearcutting as a stand-replacing disturbance mechanism create similar dynamics.

MATERIALS AND METHODS

Study Area

The study was conducted in the boreal forest north of Lake Superior and west of Lake Nipigon in a transition between the Superior (B.9) and the Upper English River (B.11) Forest Regions (Rowe 1972), approximately 150 km north of Thunder Bay, Ontario (48° 22' N, 89° 19' W, 199 m elevation). The study area has a moderately dry, cool climate with short summers. The average annual precipitation for Thunder Bay (1971-2000) is 712 mm and the average annual temperature is 2.5 °C (Environment Canada 2005). Topographic features were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago.

Rowe (1972) described the forest of the region as containing a mix of paper birch, trembling aspen, balsam fir, white spruce and black spruce, jack pine, eastern white cedar (*Thuja occidentalis* L.), and tamarack (*Larix laricina* (Du Roi) K. Koch), with a small contribution on certain sites from red and white pine (*Pinus resinosa* Ait. and *Pinus strobus* L., respectively), yellow birch (*Betula alleghaniensis* Britt.), black ash (*Fraxinus nigra* Marsh.), and sugar maple (*Acer saccharum* Marsh.). The natural stand-initiating disturbance of the area is predominately stand-replacing fire, which is also the most common stand-replacing mechanism in the boreal forest (Johnson 1992).

The methods of clearcutting varied depending on the year(s) when harvesting occurred. In the 7 year-old stands I sampled, trees were felled and dragged to roadside for processing. In the 25-31 year-old stands, trees were cut down and topped and limbed at the stump before being dragged to roadside (Paul Poschmann, *personal communication*).

Clearcut stands then underwent post-logging silvicultural prescriptions depending on the desired composition of the post-disturbance stand and the composition of the pre-disturbance stand. Stands that were dominated by trembling aspen before clearcutting were left to develop naturally, causing the post-disturbance stand to become largely dominated by trembling aspen. Stands that were dominated by jack pine prior to clearcutting were seeded with jack pine and aerial-sprayed with herbicide to reduce competing vegetation. Mixedwood stands were also seeded with jack pine. However, these stands were either not treated with a herbicide spray or herbicide treatment was not successful, resulting in a large proportion of trembling aspen on these sites. Paper birch and balsam fir were also found in various sizes and proportions in jack pine, trembling aspen, and mixedwood stands of clearcut origin.

Sampling Design

I studied three stand types: 1) conifer dominated by jack pine at early stages of development and a mixture of black spruce, white spruce, and balsam fir at later stand development, 2) broadleaf dominated by trembling aspen at early stages of development and paper birch at later stand development, and 3) mixedwood which consisted of a mixture of trembling aspen and jack pine in early stages of development and a mixture of black spruce, white spruce, balsam fir, and paper birch at later stages of development. Stands were selected using random stratified sampling along a chronosequence from stands of fire-origin with ages ranging from 7 to 201 years and clearcut ranging from 7 to 31 years (Appendix I, II). The oldest clearcut stands located in the study area were 31 year-old, since clearcutting has only occurred for approximately that time in the study area (Paul Poschmann, *personal communication*). The determination of stand type was based on a modification of methodology used by Greif and Archibold (2000). Stands were assessed as belonging to a specific stand type based on the density of conifer trees that dominated the overstory of the stand. Stands with greater than 75% conifer component were classified as "conifer type", stands with 25-75% conifer component were classified as "mixedwood type", and stands with less than 25% conifer component were classified as "broadleaf type".

The disturbance origin for each plot was determined through forest resource inventory information, silvicultural records, and provincial fire disturbance maps. Verification in the field was done by visually estimating CWD and tree density.

In order to limit soil variability, all stands were sampled on prevailing mesic, upland sites with a slope < 10%. On each site, a soil pit was dug using methods outlined by British Columbia Ministry of Environment and British Columbia Ministry of Forests (1998) and assessment followed Sims *et al.* (1997) and Soil Classification Working Group (1998). For all sites, the soil order was Brunisol with sandy loam, sandy clay loam, or clay loam soil texture.

In total, 69 stands were sampled. Mixedwood stands of approximately 139 years of age were not available for sampling in the study area. This gap in mixedwood stand age is likely caused by the infrequency of fire in the study area which resulted in narrowed sampling possibilities.

Field Measurements

Tree ages were used to estimate the time since last stand-replacing disturbance (TSD) (Bergeron 1991), with the exception of the 7 and 25 year-old fire-origin and 7 and 25-31 year-old clearcut stands where records for harvesting and fire were available. For all sampled stands, either post-fire jack pine or trembling aspen trees were selected for determination of TSD. For each of the fire-origin stands aged 72-139, no fewer than three canopy stems were sampled. For each selected tree, a core or disk taken at breast-height was brought to the laboratory for analysis. In the laboratory, the cores were mounted on constructed core strips, while disks were transversely cut and sanded to make the rings clearly visible. Rings were then counted under a microscope when needed until the same count was obtained three successive times. Tree ages were corrected to TSD by adding seven years for trembling aspen and eight years for jack pine using the model developed by Vasiliauskas and Chen (2002). For the oldest fire area (i.e., 201 year-old stands), one live jack pine tree and three jack pine snags were sampled and disks were cut at the base of stems. The ring count of the live tree was 201 years and that of snags ranged 140 to 180 years. I used the live tree age as TSF for the area.

A 400 m^2 circular plot was established for representative sampling within each stand. Within each plot, the diameter at breast-height (DBH) (1.3 m above the root collar), height, and species of all snags (DBH $\geq$10 cm, height $\geq$2 m, <45° vertical lean, and no living foliage; *sensus* Lee *et al.* (1997)) were measured and recorded.

A line-intercept method was used to sample DWD at each site (Van Wagner 1968; De Vries 1974). Two 50 m long transects were used that radiated out from the centre of the site with the first transect orientated in a random direction and the second one established at a 90° angle from the first transect (Woldendorp *et al.* 2004). The intercept-diameter ($\geq$2 cm; modified from Lee *et al.* (1997)), species, and decay class of all DWD that intersected the transects were recorded. In total, 4512 pieces of DWD were sampled. The classification system of decay classes were adapted as reported in British Columbia Ministry of Environment and British Columbia Ministry of Forests (1998) (Table 4.1)

Morphological characteristics were used to identify DWD to species level. which included: (A) branching pattern (up for jack pine and trembling aspen; parallel or downward for black and white spruce and balsam fir), (B) presence of papery longer-lived bark (indicating paper birch or balsam fir), (C) colour and texture of the wood (broadleaf species had whitish and conifer reddish wood colour; jack pine wood texture was 'more blocky' than other conifers), (D)

Table 4.1. Decay classes and descriptions for downed woody debris (British Columbia Ministry of Environment and British Columbia Ministry of Forests (1998)).

Characteristic	Class 1	Class 2	Class 3	Class 4	Class 5
Wood texture	Intact, hard	Intact, hard to partly decaying	Hard, large pieces, partly decaying	Small, blocky pieces	Many small pieces, soft portions
Portion on ground	Elevated on support points	Elevated but sagging slightly	Sagging near ground, or broken	All of log on ground, sinking	All of log on ground, partly sunken
Twigs <3 cm (if originally present)	Present	Absent	Absent	Absent	Absent
Bark	Intact	Intact or partly missing	Trace	Absent	Absent
Shape	Round	Round	Round	Round to oval	Oval
Invading roots	None	None	In sapwood	In heartwood	In heartwood

bark and foliage features (Farrar 1995), and (E) larger size potential of jack pine and trembling aspen DWD.

Calculations

Individual snag volumes were estimated from measured DBH and height using Honer's (1983) species-specific volume equations (eq. 1):

[1] $$V = \frac{0.0043891 \times (DBH)^2 \times (1 - 0.04365 \times b_2)^2}{c_1 + 0.3048 \times \frac{c_2}{H}}$$

where V is snag volume (m^3), DBH is diameter at breast-height (cm), H is snag height (m), and b_2, c_1, c_2 are species-specific parameters. Individual snag volumes were summed to the plot level and then scaled to per hectare. Basal area of individual snags was calculated using the following (eq. 2):

[2] $$BA = \pi(DBH/2)^2$$

where BA is the basal area (m^2) of an individual snag and *DBH* (m) is the diameter of the snag at breast-height. Individual BA values were also summed to the plot level and then scaled to per hectare. Densities of snags were obtained by counts per plot and then scaled to per hectare.

Downed woody debris volume was calculated using the formula described by Van Wagner (1968) (eq. 3):

[3] $$V = \frac{\pi^2 \sum d^2}{8L}$$

where V is volume (m^3/ha), d is intersection diameter (cm) of each piece of DWD, and L is the length (m) of the transect. Linear counts (number of pieces per 100 m transect) of DWD were determined and used to obtain an estimate of DWD density (Harper *et al.* 2005).

Statistical Analysis

Since my clearcut chronosequence was much shorter than that of fire-origin, I conducted my analysis in two steps. I first determined if snag and DWD volume and density differed in 7 to 201 year-old fire-origin stands by TSF (continuous variable) and stand type (categorical variable). The following multiple polynomial regression model was used (Neter *et al.* 1996) (eq. 4):

[4] $$I' = b_o + b_1 A + b_2 A^2 + b_3 A^3 + b_4 T + b_5 AT + b_6 A^2 T + b_7 A^3 T$$

where I' is predicted volume, BA, and density, b_i are coefficients, A is TSF (years), and T is stand type. A third-order polynomial model was found to best describe the CWD accumulation pattern in this study. A fourth-order polynomial model was not more significant than the third-order model due to the insignificance of the fourth-order.

Second, I examined if snag and DWD volume, BA, and density differed with TSD, stand type, and stand origin (categorical variable) between 7 to 25 year-old fire-origin and 7 to 31 year-old clearcut stands, using the following model (Neter *et al.* 1996) (eq. 5):

$$[5] \qquad I' = b_o + b_1 A + b_2 T + b_3 O + b_4 AT + b_5 AO + b_6 TO + b_7 ATO$$

where I' is predicted volume and density, b_i are coefficients, A is TSD (years), T is stand type, and O is stand origin. Normality and homogeneous variances were confirmed following Neter *et al.* (1996). Statistical significance was based on $\alpha = 0.10$ and all statistical analysis was performed using SYSTAT® 10 2000 (SPSS Inc. 2000). Since analysis indicated that snag BA and density responded similar to snag volume and DWD density responded similar to DWD volume, I only reported snag volume and DWD volume here.

RESULTS

CWD Dynamics of Fire-Origin Stands along a Chronosequence

Snag volume differed with stand age and type, while DWD volume changed with stand age but not type from 7 to 201 years TSF (Table 4.2, Figure 4.1). Snag volume, regardless of stand type was highest in 7 year-old stands and decreased to a minimum in 25 year-old stands before increasing in 72-90 year-old stands (Figure 4.1A). In conifer stands, the increase in snag volume continued from 90 to 201 years TSF, whereas snag volume in mixedwood and broadleaf stands remained relatively unchanged (Figure 4.1A). In 7 year-old stands, mixedwoods had higher snag volume than both broadleaf and conifer stands, while snag volume was similar regardless of stand type in 25 year-old and 72-90 year-old stands, respectively. Conifer stands had higher snag volume compared to broadleaf stands in 139 year-old stands and had the highest snag volume in 201 year-old stands (Figure 4.1A). Downed woody debris volume accounted for

Table 4.2. Effects of time since fire (A) (years) and stand type (T) (C = conifer, M = mixedwood, and B = broadleaf) on snag and downed woody debris (DWD) volume (m^3/ha) in 7 to 201 year-old fire-origin stands.

Source	df	Snag volume (m^3/ha)			DWD volume (m^3/ha)		
		MS	F	P	MS	F	P
A	1	105251	77.3	<0.001	72860.1	31.4	<0.001
A^2	1	86049.9	63.2	<0.001	55746.3	24.0	<0.001
A^3	1	77444.6	56.8	<0.001	48723.8	21.0	<0.001
C	2	35701.3	26.2	<0.001	1602.1	0.7	0.508
A x T	2	28508.9	20.9	<0.001	1488.4	0.6	0.532
A^2 x T	2	26086.4	19.1	<0.001	2092.9	0.9	0.414
A^3 x T	2	25069.8	18.4	<0.001	2369.1	1.0	0.367
Error	39	1362.4			2321.8		

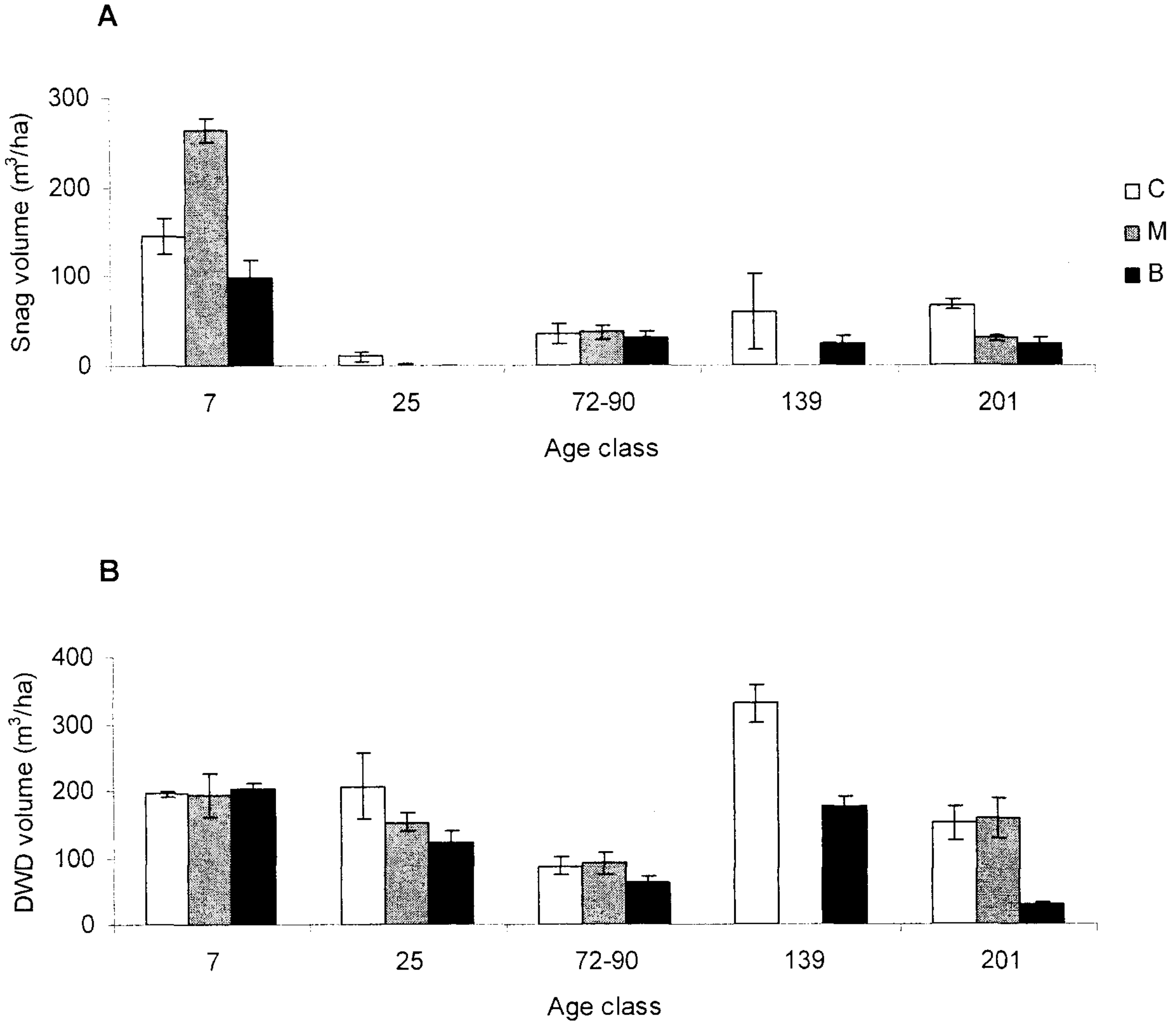

Figure 4.1. Relationships between (A) snag and (B) downed woody debris (DWD) volume (m^3/ha) and stand age class (years) and stand type in fire-origin stands. Symbols represent C = conifer, M = mixedwood, and B = broadleaf. Error bars represent ± standard error of the mean. No data is available for the 139 year-old mixedwood age class.

most of CWD volume for all age classes except in 7 year-old stands. Despite the differences of snag volume among stand types, DWD volume in all stand types was similar in 7 and 25 year-old stands, decreased to a minimum in 72-90 year-old stands, increased in 139 year-old stands and decreased again in 201 year-old stands (Figure 4.1B). Across the three stand types, CWD volume (the sum of snag and DWD volume) varied at 320-480 m^3/ha in 7 year-old stands, 100-200 m^3/ha in 25 year-old, 80-100 m^3/ha in 72-90 year-old, 200-400 m^3/ha in 139 year-old, and 50-200 m^3/ha in 201 year-old stands.

Regardless of stand type, composition of snag volume shifted as stand age increased from 25 to 201 years TSF from being dominated by early successional tree species (jack pine and trembling aspen) to being dominated by later successional tree species (white and black spruce, balsam fir, and paper birch) (Figure 4.2). The species composition of snags in 7 year-old stands reflected the species composition of the pre-disturbance stands, indicating almost exclusively early successional jack pine in conifer stands (Figure 4.2A) and a mixture of early successional jack pine and trembling aspen and late successional white and black spruce and paper birch in mixedwood and broadleaf stands (Figure 4.2B,C). Downed woody debris responded similar to snags with stand age and type (Figure 4.3).

Composition of decay classes in DWD differed with stand age and type (Figure 4.4). As stand age increased from 7 to 201 years TSF, DWD was less decayed, more decayed, then less and more decayed again in conifer stands (Figure 4.4A). The decay of DWD responded similar in mixedwood as in conifer stands with stand age (Figure 4.4B). In broadleaf stands, the change in decay composition with stand age was however less apparent as there were significant volumes of DWD in all decay classes from 25 to 201 years TSF with intermediate decay being most common (Figure 4.4C).

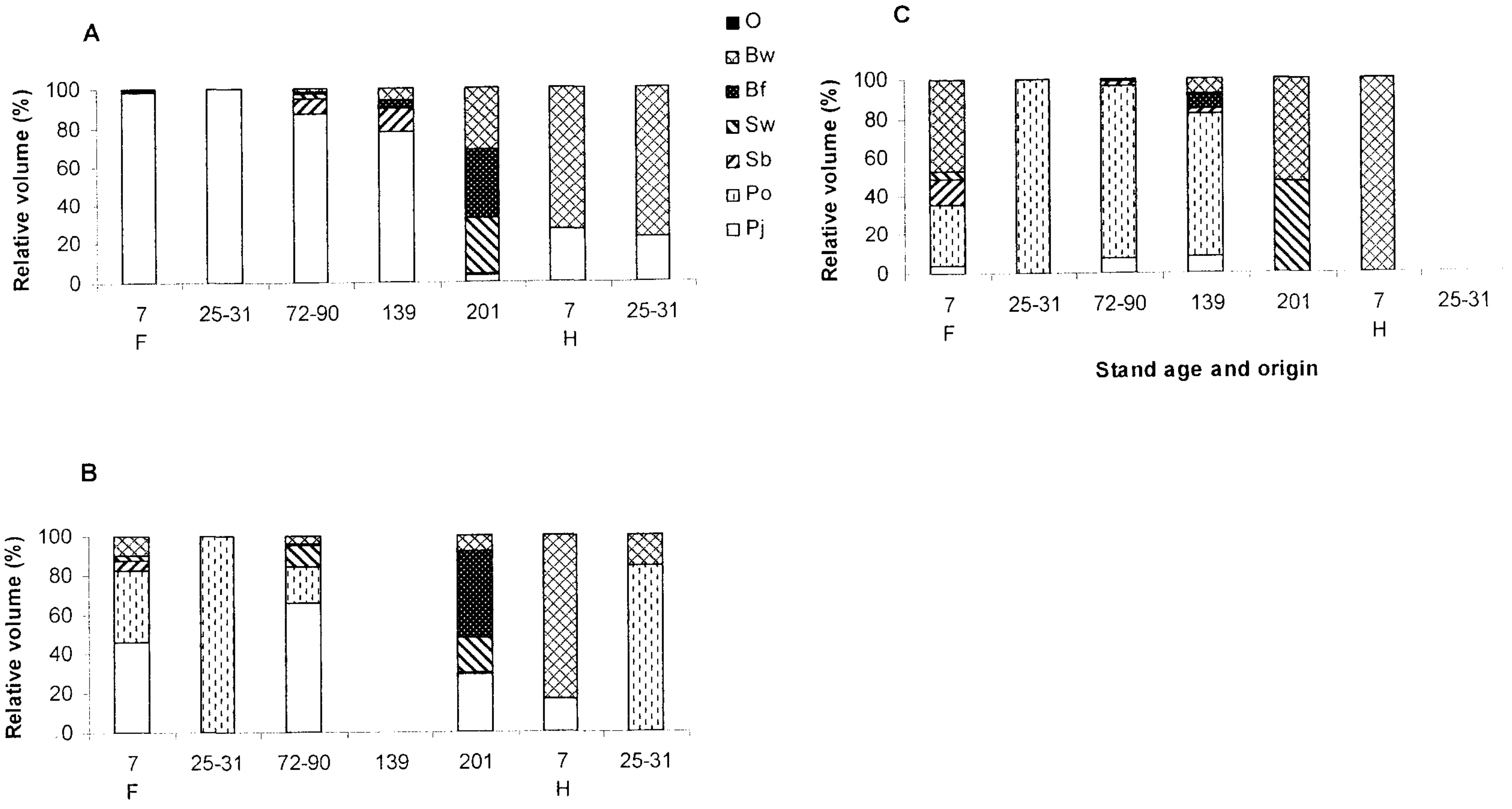

Figure 4.2. Relative snag volume (%) by species (O = other, Sw = white spruce, Sb = black spruce, Pj = jack pine, Po = trembling aspen, Bw = paper birch, and Bf = balsam fir), stand age class (7, 25-31, 72-90, 139, and 201 year-old stands), and stand origin (H = clearcut and F = fire) in (A) conifer, (B) mixedwood, and (C) broadleaf stands. No snags occurred in the 25-31 year-old broadleaf clearcut stands. No data is available for the 139 year-old mixedwood age class.

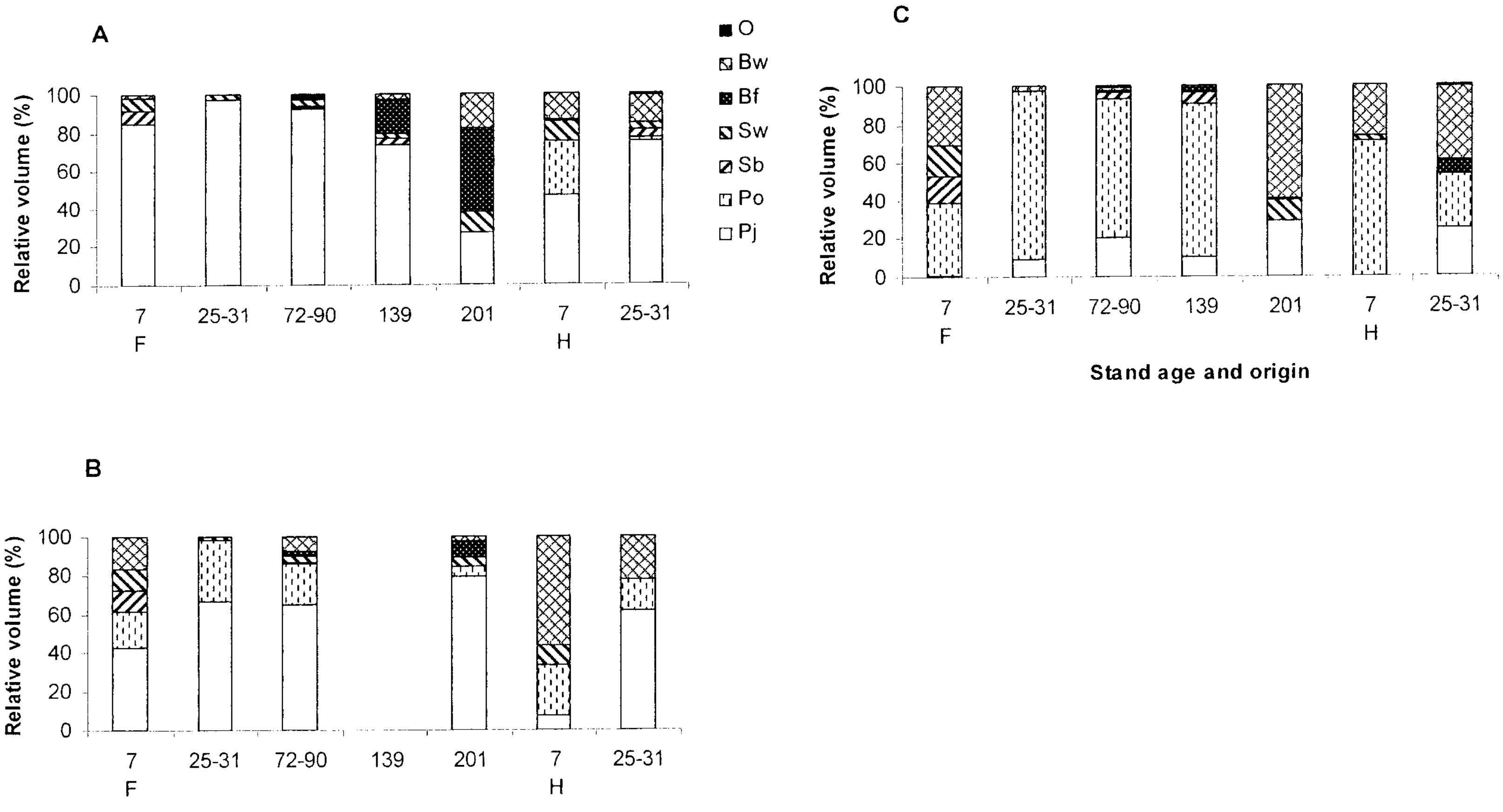

Figure 4.3. Relative downed woody debris volume (%) by species (O = other, Sw = white spruce, Sb = black spruce, Pj = jack pine, Po = trembling aspen, Bw = paper birch, and Bf = balsam fir), stand age class (7, 25-31, 72-90, 139, and 201 year-old stands), and stand origin (H = clearcut and F = fire) in (A) conifer, (B) mixedwood, and (C) broadleaf stands. No data is available for the 139 year-old mixedwood age class.

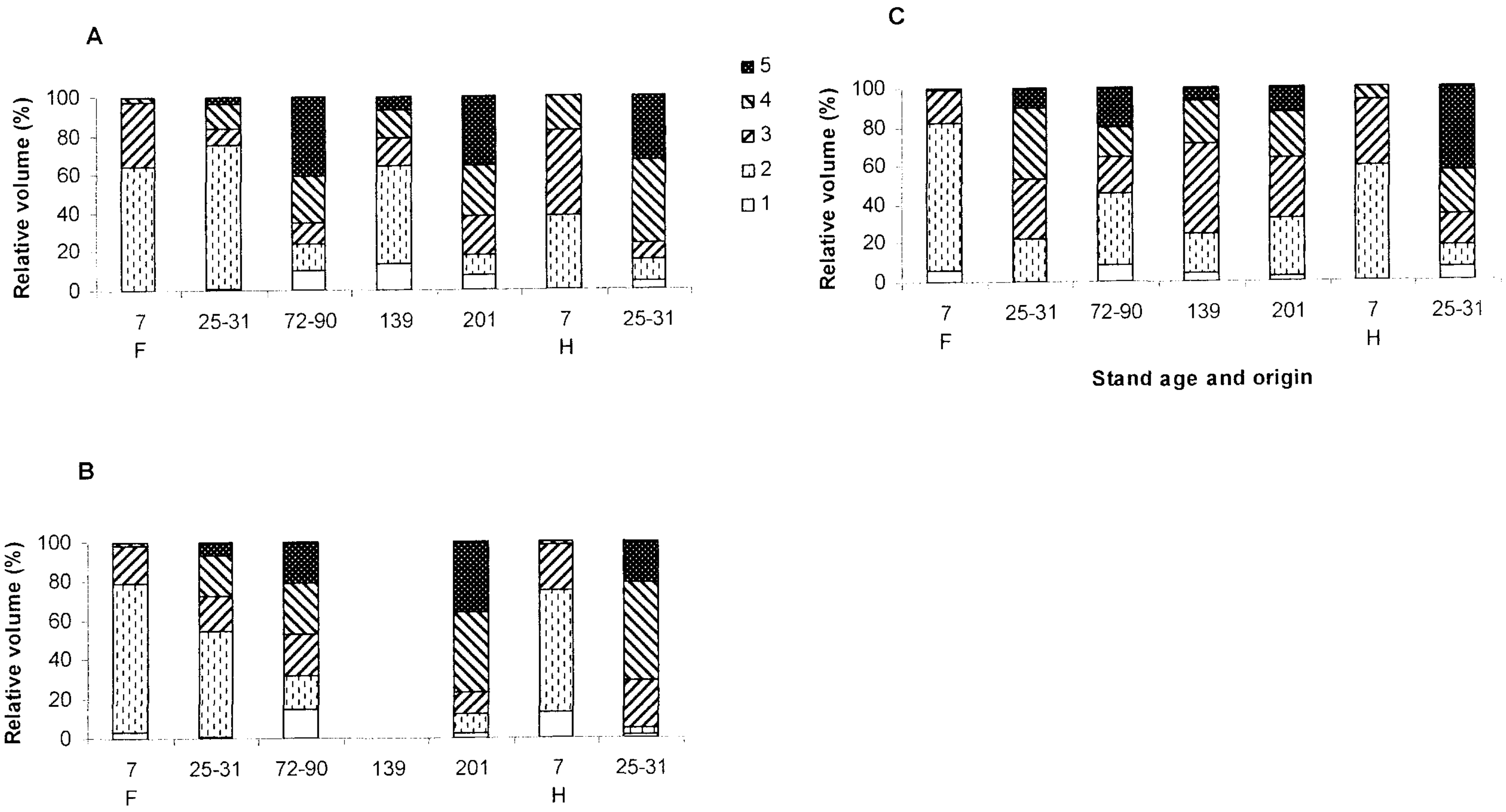

Figure 4.4. Relative downed woody debris volume (%) by decay class (see Table 4.1 for decay class descriptions), stand age class (7, 25-31, 72-90, 139, and 201 year-old stands), and stand origin (H = clearcut and F = fire) in (A) conifer, (B) mixedwood, and (C) broadleaf stands. No data is available for the 139 year-old mixedwood age class.

Stand Origin effects on CWD Dynamics

Stand origin as well as stand type and age significantly influenced snag and DWD volume (Table 4.3, Figure 4.5). Regardless of stand type, fire-origin stands had significantly higher CWD volume compared to clearcut stands, most significantly as a form of snags in 7 year-old stands and DWD in both 7 and 25-31 year-old stands (Figure 4.5). For fire-origin stands, CWD volume was significantly higher in 7 year-old stands than in 25-31 year-old stands, attributed to ten- to one hundred-fold more snags in the younger stands. However, in clearcut stands, the differences in snag and DWD volume between age classes were much less apparent (Figure 4.5).

Table 4.3. Effects of time since disturbance (A) (years), stand type (T) (C = conifer, M = mixedwood, and B = broadleaf), and stand origin (O) (H = clearcut and F = fire) on snag and downed woody debris (DWD) volume (m3/ha) in 7 to 25 year-old fire-origin and 7 to 31 year-old clearcut stands.

Source	df	Snag volume (m^3/ha)			DWD volume (m^3/ha)		
		MS	F	P	MS	F	P
A	1	81373.1	307.4	<0.001	3810.0	2.8	0.109
T	2	11611.2	43.9	<0.001	98.0	0.1	0.931
O	1	121780.5	460.0	<0.001	73811.9	53.7	<0.001
A x T	2	7305.5	27.6	<0.001	988.7	0.7	0.497
A x O	1	76868.4	290.4	<0.001	3889.4	2.8	0.106
T x O	2	10726.6	40.5	<0.001	1770.3	1.3	0.294
A x T x O	2	7234.9	27.3	<0.001	3759.9	2.7	0.085
Error	24	264.7			1374.7		

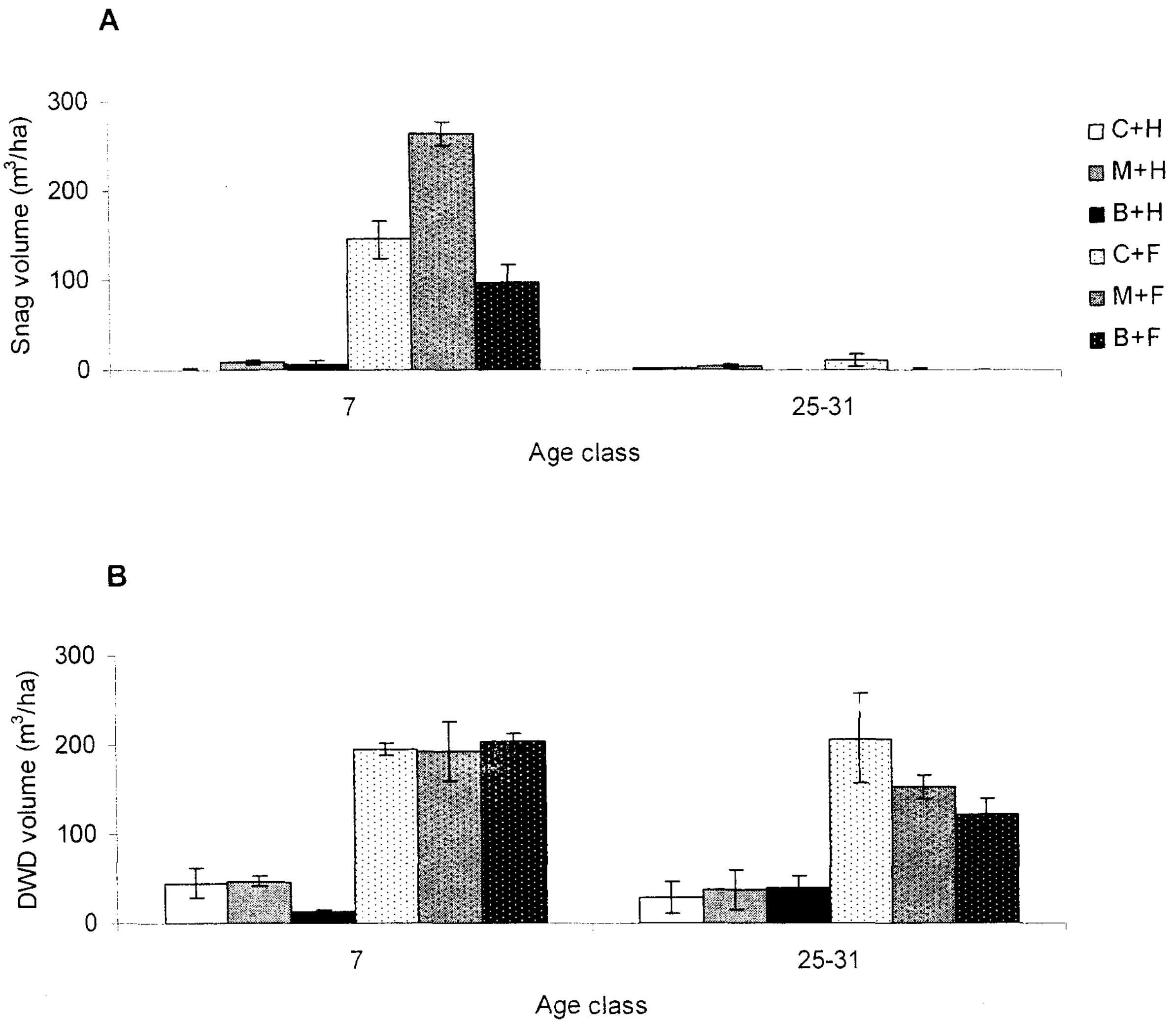

Figure 4.5. Relationships between (A) snag and (B) downed woody debris (DWD) volume (m^3/ha) and stand age class (years), stand type, and stand origin. Symbols represent C+H = conifer clearcut, M+H = mixedwood clearcut, B+H = broadleaf clearcut, C+F = conifer fire-origin, M+F = mixedwood fire-origin, and B+F = broadleaf fire-origin. Error bars represent ± 1 standard error of the mean.

Clearcut and fire-origin stands differed in their snag and DWD species compositions and DWD decay status. For all three stand types, in both 7 and 25-31 year-old clearcut stands, there was a greater proportion of paper birch snags in comparison to respective fire-origin stands (Figure 4.2). The same trend was found for DWD (Figure 4.3). Regardless of stand type, in both

7 and 25-31 year-old stands, DWD in fire-origin stands was generally less decayed than clearcut stands (Figure 4.4). An exception was the 7 year-old mixedwoods where the distribution of DWD volume by decay class was similar in clearcut and fire-origin stands (Figure 4.4B).

DISCUSSION

CWD Dynamics of Fire-Origin Stands along a Chronosequence

The dynamics of CWD in a stand in this region of the boreal forest are influenced by factors that cause (1) CWD inputs (i.e., fire, competition during self-thinning, longevity-related mortality, insects, diseases, and blowdown) and CWD losses (i.e., fire and decay) (Lee *et al.* 1997; Clark *et al.* 1998; Greif and Archibold 2000; Chen and Popadiouk 2002; Brassard and Chen 2006). Shortly after fire, snag volume is very high, a consequence of the stand-replacing fire that kills most (if not all) of the trees in a stand. In the 7 year-old age class where the snags are pre-fire in origin, the greater amount snag volume in mixedwoods than conifer and broadleaf stands may be largely attributed to that mixedwoods have a greater productivity and support a greater number of trees per unit area (MacPherson *et al.* 2001; Chen *et al.* 2003; Légaré *et al.* 2005), whereas differential rates of falling between conifer and broadleaf snags may have also affected the amount of snags observed in this age class.

During the first few decades following fire, snags decay and episodically fall, causing snag volume to decrease to very low values. The episodic falldown of snags and the persistence of large-sized DWD that survived the fire maintain a high DWD volume during the first few decades following fire. Among stand types, a higher amount of DWD in conifer stands may be attributed to that conifer tree species have slower rates of decomposition compared to broadleaf tree species (Harmon *et al.* 2000; Yatskov *et al.* 2003).

Later during stand development, the beginning of longevity-related canopy tree mortality would commence the production of larger-sized snags, causing snag volume to increase. During the beginning period of stand canopy transition, i.e., 72-90 year-old stands, snag and DWD volumes were low, as the high volume of fire-generated DWD would have almost completely decayed (Lee *et al.* 1997; Sturtevant *et al.* 1997; Clark *et al.* 1998; Hély *et al.* 2000a; Brassard and Chen 2006), and smaller-sized DWD generated by self-thinning (Greif and Archibold 2000) would decay rapidly and therefore not persist in the stand for long. As stand age further increases, and canopy breakup of the pioneering cohort is nearly complete (Chen and Popadiouk 2002), DWD volume becomes high again, as these large, old jack pine and trembling aspen trees fall and contribute to the DWD pool. Though jack pine is considered to be a longer-lived tree species than trembling aspen (Burns and Honkala 1990; Farrar 1995), I observed canopy breakup occurred sooner in my jack pine-dominated conifer stands compared to my trembling aspen-dominated broadleaf stands, which reflects the significantly higher DWD volume in conifer compared to broadleaf stands in the 139 year-old age class.

As the pioneering cohort completely dies off and stands become dominated by later successional trees species (Chen and Popadiouk 2002; Brassard and Chen 2006), snags would be generated by both competition- and longevity-induced tree mortality as well as periodic insect outbreaks and diseases. In my 201 year-old conifer stands, the dominance of spruce budworm host-specific balsam fir and white and black spruce trees (Blais 1981; Morin 1994; MacLean and MacKinnon 1997; Bergeron and Leduc 1998; Bouchard *et al.* 2005) likely contributed to the over 2-fold greater snag volume in conifer compared to mixedwood and broadleaf stands. The susceptibility of spruce and fir to spruce budworm may also explain a similar snag volume trend among stand types in the 139 age class.

While the high volumes of DWD generated by canopy break-up would have largely decayed by this stage of development, continuous inputs of DWD occur as a consequence of the snag-generating processes discussed in the above paragraph. The significantly lower DWD volume occurring in broadleaf stands compared to conifer and mixedwood stands is attributed to (1) the higher decomposition rates of broadleaf tree species that would have resulted in (a) almost complete decomposition of DWD generated by canopy breakup that had taken place approximately 50 years ago and (b) DWD generated by the death of dominating paper birch canopy trees persisting for only a relatively short period of time (Harmon *et al.* 2000; Yatskov *et al.* 2003) and (2) the non-host specificity of paper birch to spruce budworm.

For all three stand types, I found that species replacement patterns for snags and DWD proceeded from 7 to 201 years TSF from a greater proportion of early successional species to a greater proportion of later successional species. Coarse woody debris species replacement with TSF reflect canopy succession, where early successional tree species give way to later successional tree species as TSF increases (Bergeron and Dubuc 1989; Bergeron and Dansereau 1993; Bergeron 2000; De Grandpré *et al.* 2000; Gauthier *et al.* 2000). Once a tree dies, its joins the CWD pool as either a snag or DWD. Therefore, though CWD species replacement patterns likely lag behind tree succession, it is not surprising that species replacement patterns for both follow similar trajectories of Douglas-fir (*Pseudotsuga menziesii* (Mirb.))-dominated forests in western Oregon and Washington, USA reported by Spies *et al.* (1988) and of mixedwood forests in northwestern Quebec, Canada reported by Hély *et al.* (2000a).

Stand Origin effects on CWD Dynamics

It is evident that the dynamics in the stands I studied differed greatly between stand-replacing disturbance mechanisms (fire and clearcutting). In contrast to fire as discussed above, clearcut operations remove trees for commercial usage, leaving only small amounts of logging slash and 'undesirable' tree species on the ground and few residual trees and snags (Spies *et al.* 1988; Sippola *et al.* 1998; McRae *et al.* 2001), resulting in relatively low CWD volume following clearcutting. Though residual trees and snags provide some CWD input, it is expected that CWD volume in clearcut stands would continue to be low until later in stand development when self-thinning would begin to generate CWD as snags initially and later DWD. However, these CWD inputs are expected to be relatively small-sized (Greif and Archibold 2000), and will not persist for long in a stand. Significant CWD inputs may not be expected to occur until longevity-related canopy tree mortality takes place much later in stand development.

The present findings that clearcut stands contained a greater proportion of paper birch snags and DWD is likely due to the fact that paper birch has low economic value, and therefore left standing following logging to meet harvesting guidelines for snag retention (Ontario Ministry of Natural Resources 2001) if equipment operators are given the choice between harvesting paper birch and a more valuable tree species. However, as paper birch decays more rapidly compared to conifers (Harmon *et al.* 2000; Yatskov *et al.* 2003), leaving a greater percentage of conifer snags may provide increased habitat opportunities for many species of birds and subnivean-requiring mammals that rely on snags and DWD.

Forest Management Implications and Recommendations for Attaining a Natural CWD Structure in Clearcut Stands

The brief history of commercial clearcutting in the study area makes a comparison of older clearcut and fire-origin stands impossible. Although pre-disturbance CWD would completely decay at some point during succession regardless of the stand-replacing disturbance mechanism, it may be expected that it would take longer for CWD to completely decay in fire-origin stands due to their higher CWD volume and larger-sizes compared to clearcut stands. For clearcutting to be economically viable, many pre-disturbance CWD characteristics could never be similar in post-clearcut as in post-fire stands.

While younger clearcut and fire-origin stands differed in their CWD dynamics, it is possible that CWD dynamics in boreal fire-origin and clearcut stands may converge as stand age increases. In theory, if the processes that generate post-disturbance CWD (self-thinning, longevity-related mortality, insects, diseases and blowdown) are similar in post-fire and post-clearcut stands, these stands would have similar CWD dynamics beyond some stand age or stage of development when pre-fire CWD would disappear. Since longevity-related mortality is species-specific and insect attacks, diseases, and blowdown are episodic events, it is possible that CWD dynamics in post-fire and post-clearcut stands would develop similarly if forest management focuses on controlling stand density and composition. I recommend silvicultural prescriptions that would produce similar stand densities and composition in post-clearcut to post-fire stands immediately proceeding the polewood self-thinning stage (40-60 years TSD; Paul Poschmann, personal communication) when CWD inputs are large enough in size to persist in a stand for a significant length of time. Although managing for stand density in post-clearcut stands earlier in development would produce even greater similarity in post-disturbance CWD dynamics, the associated high cost would make it economically unsound. Establishment of permanent sample plots to monitor the CWD dynamics in post-clearcut stands would allow forest managers and scientists to determine if CWD structure becomes similar to that in fire-origin stands as TSD increases.

CHAPTER FIVE GENERAL CONCLUSIONS

The findings of my thesis confirm that many stand structural characteristics vary with stand age, composition, and origin. A summary of my research findings and conclusions and management implications and recommendations are as follows:

(1) In fire-origin stands aged 72 to 201 years time since fire (TSF), stand volume of trees differed with TSF with a U-shaped pattern in conifer stands, an inverse U-shaped pattern in broadleaf stands, but it did not change in mixedwoods. Tree density showed a U-shaped pattern with TSF for all stand types. Diameter at breast-height-based Shannon's index, applied to tree and snag data indicated that mixedwood stands were most diverse followed by conifer and then broadleaf stands while no TSF effect was found. Height-based Shannon's index showed that structural diversity peaked at a TSF of 139 years in broadleaf stands but was unaffected by TSF in conifer and mixedwood stands. While diameter at breast-height (DBH)-based coefficient of variation (CV) had a similar trend as height-based Shannon's index, height-based CV indicated highest diversity at a TSF of 139 years regardless of stand type.

(2) In fire-origin stands aged 7 to 201 years TSF, coarse woody debris (CWD) volume showed a sigmoid accumulation pattern with stand age. Contributions of snag and downed woody debris (DWD) volume to CWD volume differed with stand age and type. Snag volume, regardless of stand type was highest in 7 year-old stands and decreased to a minimum in 25 year-old stands before increasing in 72-90 year-old stands. In conifer stands, the increase in snag volume continued from 90 to 201 years TSF, whereas snag volume in mixedwood and broadleaf stands remained relatively unchanged. Downed woody debris volume in all stand types was similar in 7 and 25 year-old stands, decreased

to a minimum in 72-90 year-old stands, increased in 139 year-old stands and decreased again in 201 year-old stands.

(3) As stand age increased from 25 to 201 years in fire-origin stands, species composition of CWD shifted from dominance by early successional tree species to dominance by later successional trees species, reflecting tree species successional trajectories. Composition of DWD decay status also varied with stand age and type.

(4) In post-clearcut stands, CWD volume was smaller compared to post-fire stands, mostly in the form of noncommercial tree species such as paper birch that were in more advanced status of decay.

(5) Forest management activities could (a) increase vertical structural diversity by lengthening the harvest rotation and/or altering partial-harvesting objectives, (b) manage stand density in post-clearcut stands so that the dynamics of post-fire and post-clearcut stands converge as stand age increases, and (c) leave a greater proportion of coniferous residual trees following harvesting so CWD would persist for longer in the developing post-clearcut stand.

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APPENDICES

CHARACTERISTICS FOR 69 STANDS IN NORTHWESTERN ONTARIO, CANADA.

Number of stands sampled	Age class (years)	Stand type[*]	Stand origin[†]	Volume (m^3/ha)			Density[§]		
				Snags	DWD[‡]	Trees	Snags	DWD	Trees
3	7	C	H	0.8 (0.5)[‖]	45.0 (16.5)	NA[◊]	16.7 (8.3)	38.3 (4.1)	NA
3	25-31	C	H	1.8 (1.2)	29.1 (18.0)	NA	16.7 (8.3)	20.3 (2.4)	NA
3	7	M	H	8.9 (2.7)	47.3 (5.9)	NA	66.7 (22.0)	38.7 (3.0)	NA
3	25-31	M	H	4.5 (2.7	37.2 (21.9)	NA	50.0 (38.2)	19.3 (5.2)	NA
3	7	B	H	6.1 (4.3)	12.4 (2.2)	NA	58.3 (30.0)	18.7 (0.3)	NA
3	25-31	B	H	0.0 (0.0)	29.2 (14.7)	NA	0.0 (0.0)	27.3 (0.9)	NA
3	7	C	F	145.6 (21.1)	195.6 (5.8)	NA	650.0 (52.0)	101.3 (4.4)	NA
3	25	C	F	10.2 (6.5)	207.5 (49.8)	NA	50.0 (25.0)	140.7 (13.8)	NA
6	72-90	C	F	36.5 (11.1)	87.8 (12.5)	272.6 (18.4)	354.2 (88.6)	50.5 (6.7)	1212.5 (133.7)
3	139	C	F	59.9 (42.8)	330.1 (29.0)	139.8 (19.2)	216.7 (84.6)	87.7 (2.9)	508.3 (41.7)
3	201	C	F	67.8 (6.0)	150.9 (25.7)	238.1 (8.1)	591.7 (108.3)	65.7 (1.2)	908.3 (260.3)
3	7	M	F	264.5 (12.7)	193.9 (33.3)	NA	941.7 (36.3)	114.7 (5.4)	NA
3	25	M	F	0.6 (0.6)	153.5 (13.9)	NA	8.3 (8.3)	110.3 (4.7)	NA
6	72-90	M	F	37.4 (7.5)	92.0 (16.5)	275.8 (25.0)	425.0 (74.2)	67.7 (8.9)	1095.8 (72.6)
3	201	M	F	30.4 (3.0)	158.5 (28.8)	232.0 (32.8)	341.7 (138.7)	57.0 (13.5)	1066.7 (96.1)
3	7	B	F	98.4 (19.4)	204.3 (8.4)	NA	791.7 (60.1)	128.3 (4.6)	NA
3	25	B	F	0.4 (0.4)	123.2 (16.8)	NA	8.3 (8.3)	77.7 (3.8)	NA
6	72-90	B	F	30.3 (7.4)	62.3 (9.2)	358.5 (17.9)	258.3 (82.1)	61.3 (4.8)	916.7 (199.8)
3	139	B	F	25.1 (7.5)	175.2 (14.4)	357.6 (58.0)	183.3 (36.3)	72.0 (2.1)	716.7 (41.7)
3	201	B	F	25.6 (6.2)	28.8 (4.5)	229.9 (14.2)	325.0 (94.6)	27.3 (2.9)	1025.0 (203.6)

[*] Stand type: C = conifer, M = mixedwood, B = broadleaf

[†] Stand origin: H = clearcut, F = fire

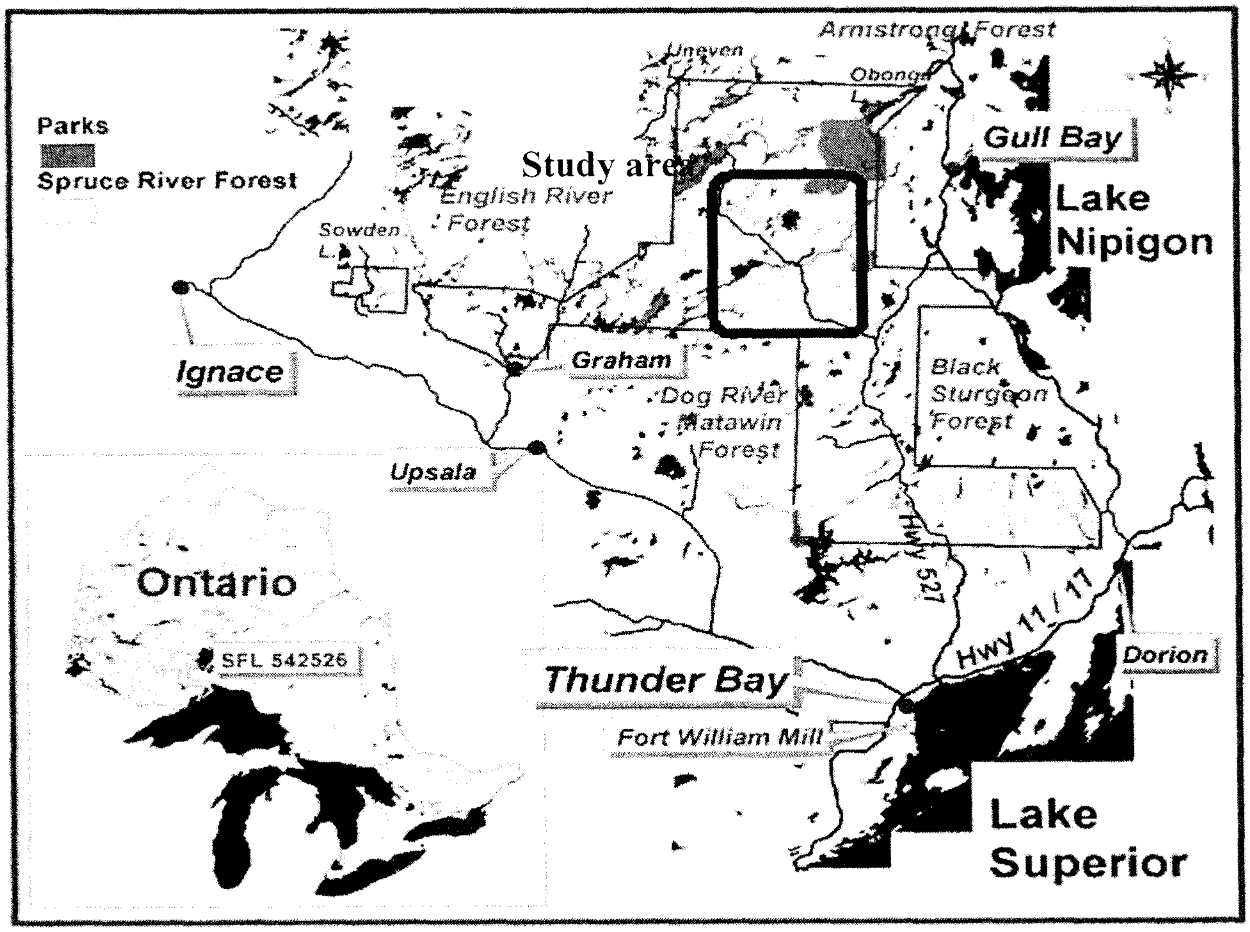
[‡] DWD = downed woody debris

[§] Density units: Trees and snags = stems/ha, DWD = pieces/100 m transect

[‖] Numbers in brackets equal to 1 standard error of the mean

[◊] Trees in 7 and 25-31 year-old age classes were too small to meet sampling criteria (DBH ≥10 cm)

MAP OF THE STUDY AREA IN NORTHWESTERN ONTARIO, CANADA.



Note: Modified from Abitibi-Consolidated (2006).